THE NEOTROPICAL LAND SNAIL GENERA LABYRINTHUS AND ISOMERIA (PULMONATA, CAMAENIDAE)

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INTRODUCTION[1]

This review of the mainland Neotropical Camaenidae had its origins in an attempt to evaluate infra-specific variation in shells of Panamanian *Labyrinthus*. It soon developed into a synoptic revision, which also serves to emphasize that 1) taxonomic knowledge of land snails is very slight; and 2) existing collections of land mollusks are totally inadequate for modern systematic research. Despite access to the major molluscan collections of the world, 48.6 per cent of the species and subspecies were represented by fewer than 10 examples, and only five taxa (7.1 per cent) by more than 100 specimens. Geographic ranges are obviously poorly understood in view of the lack of material. Actually, there are twenty-one species and subspecies (30.0 per cent) for which we lack any exact locality or for which the geographical terms are vague enough that they cannot now be placed within a fifty-mile radius. Thirteen other species (18.5 per cent) have been reported only from essentially the type locality. Many of the species in both categories are based on single collections made in the last century. For half of the taxa we scarcely have enough data for alpha taxonomy.

Because of scarcity of material and fragmentary distributional data, this paper is basically a summary of inadequate knowledge with numerous suggestions as to possibilities for research that would require field studies. Of these problems, perhaps the most important from an evolutionary viewpoint is how to classify the species. An altitudinally correlated separation into *Labyrinthus* (with the aperture grossly obstructed by teeth) and *Isomeria* (with the aperture only slightly obstructed by teeth) has been adopted, although dissections of the few available species suggest that the transition from obstructed to open aperture (or *vice versa*) happened more than once. Many distributional and ecological problems are mentioned in the body of the text.

Since the original descriptions and illustrations are scattered through publications available only in the largest libraries and mu-

[1] While this paper was in press, Chicago Natural History Museum adopted the name Field Museum of Natural History. In this paper the catalog designations remain CNHM.

seums, I have provided photographs of the shells and short diagnoses covering the main differentiating characters. The resulting synoptic review will allow identification of the species and provides available background data for field studies relating to variation and problems of classification. Perhaps the main function I can hope to serve, however, is to indicate the enormous opportunities for systematic research presented by the land mollusks and the equally great problems caused, in part, by the present lack of adequate collections.

The only previous review of the American camaenids is by Pilsbry in the Second Series of the *Manual of Conchology*. The illustrated accounts are scattered through several volumes, but summarized in Pilsbry (1894, pp. 84–143). The mainland American genera were surveyed by Pilsbry (1889, pp. 135–176). He reviewed 30 species of *Isomeria* and 22 *Labyrinthus*, compared with the 28 species in each genus recognized below. Despite having "seen scarcely half of the species" of *Isomeria*, Pilsbry's account is basically correct. Necessary alterations in synonymy are primarily caused by rediscovery of older species and examination of material collected subsequent to Pilsbry's study.

Many people are responsible for the success of this project. For permission to study all materials in collections in their charge, I am deeply indebted to Dr. Harald A. Rehder, United States National Museum; Dr. William J. Clench, Museum of Comparative Zoology, Harvard; Dr. R. Tucker Abbott, Academy of Natural Sciences, Philadelphia; Dr. E. Fischer-Piette, Muséum National d'Histoire Naturelle, Paris; Dr. H. E. Coomans, Zoologisch Museum, Amsterdam; Mr. Norman Tebble, British Museum (Natural History); Dr. A. Zilch, Senckenbergische Naturforschende Gesellschaft, Frankfurt-a.-M.; Dr. H. Burla, Zoologisches Museum der Universität, Zurich; Dr. A. Rodger Waterston, Royal Scottish Museum, Edinburgh; Dr. Tron Soot-Ryen, Zoological Museum, Oslo; and Dr. Juan Jose Parodiz, Carnegie Museum, Pittsburgh. For the loan of selected materials from their collections, I wish to thank Dr. Lothar Forcart, Naturhistorisches Museum, Basel; Dr. A. Riedel, Polska Akademia Nauk; Dr. R. Wright Barker, Houston; and Mr. Ralph Jackson, Cambridge, Maryland. Mr. Norman Tebble and Mr. John Peake, British Museum (Natural History) located and arranged for photographs of the types shown in Figure 26. I am deeply grateful to the Trustees of the British Museum (Natural History) for permission to publish these photographs. Loan of a set of types from Musee d'Histoire Naturelle de la Ville, Neuchatel, was facilitated by

Dr. L. Forcart, Basel, who visited Neuchatel to locate the specimens and arranged the requested loan.

The largest volume of material from a single source was made available by Mr. Ralph Jackson. In addition, many of the specimens in North American museums were exchanges from Mr. Jackson. Without access to his material, this paper could not have been written, since other collections contained too little material to warrant even this incomplete a study.

The many fine drawings of the apertural characters in *Labyrinthus* and most of the anatomical figures are by Miss Marian Pahl, Staff Artist of Field Museum of Natural History. Statistical calculations were made by Miss Robin Zimmerman, a student at Roosevelt University. For the laborious job of checking citations for accuracy and for typing and retyping manuscript, I am indebted to my wife and to Mrs. Rita Mecko, clerk-typist in the Division of Lower Invertebrates. Photographs were made primarily by Homer Holdren, Photographer, Field Museum of Natural History, with my assistance, or by myself during visits to other institutions.

Material

A total of 1,992 adult and juvenile specimens were examined, 1,152 belonging to species classified as *Labyrinthus* and 840 to species placed in *Isomeria*. All specimens in nine museums and one pri-

Table I

Specimens examined of *Labyrinthus*

L. triplicatus	46	*L. raimondii*	130
L. q. quadridentatus	8	*L. furcillatus*	15
L. q. biolleyi	6	*L. bifurcatus*	2
L. tamsianus	38	*L. aenigmus*	6
L. l. leucodon	44	*L. clappi*	17
L. l. umbrus	2	*L. o. otostomus*	1
L. magdalenensis	5	*L. o. bogotensis*	18
L. dunkeri	47	*L. o. assimilans*	2
L. isodon	6	*L. unciger*	121
L. vexans	3	*L. creveauxianus*	32
L. manueli	31	*L. o. otis*	33
L. sieversi	3	*L. o. orthorhinus*	268
L. sp.	2	*L. s. subplanatus*	15
L. ellipsostomus	28	*L. s. erectus*	10
L. diminutus	33	*L. s. sipunculatus*	17
L. pronus	3	*L. plicatus*	110
L. leprieurii	17	*L. marmatensis*	12
L. t. tarapotoensis	9	*L. euclausus*	—
L. t. baeri	11	*L. sharmani*	1

vate collection were examined, but only rare material, field collections, or types were borrowed from six additional sources.

TABLE II

Specimens examined of *Isomeria*

I. inexpectata	3	*I. gealei*	7
I. medemi	2	*I. aequatoria*	22
I. b. basidens	1	*I. meyeri*	—
I. b. gudeana	5	*I. oreas*	99
I. neogranadensis	1	*I. kolbergi*	101
I. bituberculata	98	*I. triodonta*	44
I. juno	56	*I. stoltzmanni*	2
I. bourcieri	65	*I. jacksoni*	20
I. hartwegi	13	*I. cymatodes*	98
I. morula	—	*I. fordiana*	5
I. anodonta	1	*I. scalena*	5
I. aloagana	—	*I. aequatoriana*	75
I. continua	16	*I. globosa*	78
I. minuta	1	*I. calomorpha*	—
I. subelliptica	3	*I. fauna*	2
I. meobambensis	16	*I. equestrata*	1

Throughout the text, the following abbreviations indicate the source of the material mentioned:

ANSP	Academy of Natural Sciences, Philadelphia
Barker	R. Wright Barker collection, Houston
Basel	Naturhistorisches Museum, Basel
Brit. Mus.	British Museum (Natural History), London
CM	Carnegie Museum, Pittsburgh
CNHM	(Chicago Nat. Hist. Mus.) Field Museum of Natural History
Edinburgh	Royal Scottish Museum, Edinburgh
Jackson	Ralph Jackson collection, Cambridge, Maryland
MCZ	Museum of Comparative Zoology, Harvard
Neuchatel	Musee d'Histoire Naturelle de la Ville, Neuchatel
Paris	Muséum National d'Histoire Naturelle, Paris
SMF	Senckenbergisches Museum, Frankfurt-a.-M., Germany
USNM	United States National Museum, Washington, D. C.
Warsaw	Polska Akademia Nauk, Warsaw
ZMA	Zoologisch Museum, Amsterdam
Zurich	Zoologisches Museum der Universität Zurich

Supplementary material of interest undoubtedly exists in the museums of Berlin, Brussels and Madrid, and several unrecognized types may remain in the unlabeled miscellany of the British Museum (Natural History), London. The types of *Isomeria morula, I. aloagana* and *I. meyeri* need to be located and refigured, but there is little doubt concerning the identity of the other species whose types were not consulted.

Shortly before this paper was sent to the printers, Dr. Lothar Forcart informed me that the Naturhistorisches Museum, Basel,

had just received the collection of the late Dr. P. Bohny, which included the conchological cabinet of the Swiss botanist Edmond Boissier (1810–1885). Included in the latter collection was type material of three *Labyrinthus*—one specimen of *L. tamsianus* received from Dunker; one specimen of *L. leprieurii* received from Petit; and two specimens of *L. unciger* received from Petit. Measurements furnished by Dr. Forcart showed the specimens fell within the range of variation reported below. Whether these specimens should be designated lectotypes or not is beyond the scope of this study, since possibly other authentic material exists in other museums.

Including *incertae sedis*, there are 70 taxa. No material could be examined of five of these; fourteen are represented by only one or two individuals; and nine by three to five examples. Thus 40 per cent of the species and subspecies are represented by less than six specimens in the major molluscan collections of the world. An additional nineteen species and subspecies are based on a sample of six to twenty individuals; seven taxa by twenty-one to forty shells; eight by forty-one to eighty; seven by eighty-one to 160; and only one unit, a subspecies (*Labyrinthus otis orthorhinus*), by more than 160 specimens. Table III indicates the representation in the larger collections where all available material was examined. Ignoring the five *incertae sedis*,

TABLE III

Representation in Collections

	CNHM	ANSP	SMF	USNM	ZURICH	EDIN-BURGH	MCZ	JACKSON
Taxa								
Labyrinthus (36)	27	27	21	25	17	16	20	4
Isomeria (29)	18	18	19	12	16	12	7	11
Total (65)	45	45	40	37	33	28	27	15
Sets								
Labyrinthus	104	77	76	84	23	18	45	12
Isomeria	74	56	78	35	23	16	17	59
Total	178	133	154	119	46	34	62	77

the collections with the greatest representation (CNHM and ANSP) had 69.3 per cent of the known species and the next most complete collection (SMF) 61.5 per cent of the taxa. The collections are strictly synoptic, CNHM averaging 3.94 sets per taxon; ANSP 2.96 sets; and USNM 3.22 sets.

Most of the sets contained only one or two specimens. The reason for this is historical. Modern museum collections consist mainly of material first obtained by amateurs and donated or sold to the institutions upon the death of the owner. Even at the present time, most amateur collectors utilize long series of shells as trade items, exchanging for species not represented in their collection. This attitude also has prevailed among museums, and many of the larger sets may represent only part of the original sample. One or two specimens from the original sample will be found in several other museum and private collections throughout the United States and foreign countries. Often a possibly unconscious bias is introduced in the process of trading such materials. I will cite examples from only one species, although several were noticed. Seventeen shells of *L. otis orthorhinus* collected on Barro Colorado Island in January, 1936 are now MCZ 111160. Two shells, formerly part of that set, are Jackson 4829, and four are in the ZMA. Others undoubtedly exist in other collections. The two in Ralph Jackson's collection and two of the four in the ZMA are smaller than all but three of the seventeen remaining in the MCZ collection. Similarly, three shells from the Salamanca Hydrographic Station set (MCZ 111166) now in the ZMA were the 2nd, 3rd and 7th smallest of the fourteen examples located. Selection of these smaller examples for "trading" undoubtedly biased the remaining sample in favor of large size. This probably explains the slightly larger (0.6 mm.) mean diameter of the MCZ Barro Colorado Island set (see Table X, p. 107), when compared with material collected in other years. Such a bias is not, of course, that simple, since "specimen quality" as well as size is involved in shell exchanges between amateurs.

The net result is that originally large samples will be widely distributed through exchange. Over the 100-year period that most of these species have been known, the sets will be reduced to scattered short series of one or two examples. In preparing such exchanges, the tendency in the past often has been to shorten the label, so that specimens originally part of the type set labeled "Frontino, Colombia at 6,000 feet elevation" (*L. aenigmus*), now are labeled "New Granada" (see p. 90). Occasionally the reverse happens. A shell of *L. aenigmus* with a collection label "New Granada" had the museum label expanded to "Andes near Frontino, Colombia."

These facts are common knowledge to museum curators, but have been presented here as a cautionary note to non-museum taxonomists who might wish to use data from the tables in statistical analy-

sis. It can be presumed that most of the sets in museum collections that contain more than six or seven examples and were collected more than ten or fifteen years ago, have had specimens "traded off" and are biased selections. Contrary to normal expectations, I feel that sets with five to six examples, usually not subject to such trading, present a more reliable sample in this study than the sets with ten or more examples.

A special note must be given concerning material from Ralph Jackson's collection. For over twenty years he has had a collecting contact in Ecuador providing land and fresh-water shells. As a result, his personal collection contains more than twice the number of *Isomeria* (251 shells) found in the largest museum collection (CNHM with 123 shells). At intervals his collector forwards material collected "in the vicinity of" a town. Mr. Jackson sometimes has had several repeated sendings over a period of several years from the same locality. These shells are grouped in the same set in his collection. This is in accord with past procedures in such museums as the University of Michigan Museum of Zoology. While this greatly reduces their utility in statistical analysis, in the absence of adequate data, any data is useful. The analysis of variation in the long sets from the Jackson collection is valid only to the extent of showing the range in variation for a species from the vicinity of a town over a period of several years. In the case of *Isomeria*, much of the material in North American museum collections has been obtained in trade from Mr. Jackson. Careful checking of these traded sets shows no size bias, but an obviously successful attempt to provide "quality" specimens to his correspondents. In many cases, the traded material has been included in the statistical analysis.

It can be argued that such biased samples and grouped year classes would make any statistical treatment of the data a waste of time. For both *Labyrinthus unciger* (Table IX, p. 101) and *L. otis orthorhinus* (Table X, p. 107), we have sets taken from the same locality at intervals over a twenty to twenty-three-year period. Size variation in these chronologically separated sets, representing several generations, is minimal. Hence, analysis of the sets has been considered necessary to give at least some idea of the range of variability. The probable extent of sample bias, however, does preclude the desirability of more sophisticated statistical analysis of the data.

The above data clearly demonstrate that only synoptic collections of *Isomeria* and *Labyrinthus* exist and that these collections are totally inadequate for modern systematics. The present sad state of

molluscan taxonomy is equally clearly demonstrated by the fact that even this inadequate material allowed major alterations in synonymies, as well as the inevitable description of four new species, one new subspecies and proposal of one new name.

Because they are large and easily spotted, these genera are, among the Neotropical land snail fauna, well represented in museum collections. For most other Neotropical taxa, much less material is available and even cruder systematic work is necessary. In order to correct this situation, massive collecting efforts are needed. Even casual collections by field zoologists interested in other groups can add valuable material at our present level of knowledge. Particularly, collection of live material with subsequent preservation of the soft parts is desirable, since only seven of the fifty-six species of *Labyrinthus* and *Isomeria* have been dissected. Equally small proportions of other Neotropical land snail taxa are known by other than the empty shell.

It took several generations of concentrated activity by bird and mammal collectors to provide adequate systematic collections of Neotropical species. No similar effort to accumulate equivalent mollusk collections seems probable, and adequate systematic work will have to depend on gradual accumulation of fortuitous collections by vertebrate zoologists, geologists, teachers and missionaries. I will be pleased to provide information on collection and preservation techniques to interested parties and will be glad to receive any Neotropical molluscan materials for deposit and study.

Early collections of birds and mammals were taken "in the vicinity of" a cited locality. For most of the land snail collections, we have not progressed from this primitive stage. Ornithologists have been particularly active in trying to elucidate the altitudinal limits covered by these early, rather nebulous collections. Since many of the original collections of land snails were by early professional zoological collectors, the papers of de Schauensee (1948, pp. 251–342) for Colombia and Chapman (1926, pp. 703–722) for Ecuador have been most helpful in indicating the probable altitudinal ranges encompassed by early localities. In the body of this study, data as to altitude have been presented without direct citation of these sources. They represent reasoned guesses as to the probable vertical range within which the shells were collected, and are in no way to be accepted as accurate citations. For other sets, apparently accurate altitudinal data were included on the field label. The resultant altitudinal ranges are thus only preliminary estimates or guesses as to the probable range. The general altitudinal separation of *Labyrinthus* and *Isomeria* is discussed

fully in the section on distribution (pp. 196–212). Here it is worthwhile to record that we have practically no information on the phenomenon of altitudinal replacement. *Labyrinthus unciger* and *L. creveauxianus* may show such replacement in Northern Colombia. In the Sierra Nevada de Santa Marta there are four species—*L. sieversi* (300–5,500 feet), *L. clappi* (4,000–5,000 feet), *Isomeria medemi* (8,200–8,850 feet) and *I. inexpectata* (8,500–9,000 feet). These species live in different parts of the mountain range, except possibly *L. clappi* and *I. medemi*, which may be altitudinally zoned. The only clear case of possible altitudinal zoning in a restricted area is the Rio Páez Valley, Huila, Colombia where *I. oreas* was collected at 2,900 meters elevation and *I. scalena* at 2,400 meters elevation.

Life History and Ecology

We have no accurate data on the length of life or the reproductive cycle. An adult of *L. otis otis* (CNHM 133263) collected January 31, 1963 laid a cluster of eight eggs that evening. The eggs were preserved in alcohol, but have not been dissected. A live nearly adult *L. unciger* taken in February, 1959 at El Valle was sexually immature (see fig. 5) even though lip formation had started. Many snails become sexually mature prior to lip formation or other indication of adulthood. Apparently this may not be the case in *L. unciger*. There are no other data available.

Numerous young shells of *L. otis orthorhinus* collected in January and February, 1959 fell into two size classes, one of about 8 mm. in diameter and the other 16.5–17.5 mm. This suggests two possibilities: first, that they represent year classes, which might indicate a three or four-year cycle from hatching to adulthood; or second, a seasonal pattern of reproduction with two broods each year in Panama during the rainy seasons. The doubling in size between the two classes (8 to 17 mm.) would indicate roughly that adult size (35–41 mm. on Barro Colorado Island) could be reached in another equal period of time. It is equally possible that two additional periods would be required, one to reach the actual diameter and the second to form the characteristic lip. While an annual, rather than a seasonal, pattern seems more probable, we have no data as to which is correct. The possible time lapse from hatching to adulthood in *L. otis orthorhinus* cannot be placed in narrower limits than 1½ to 4 years without more data. We have no information concerning the length of life in other species.

Ecological data are equally fragmentary. All material taken by myself in Panama (*L. unciger* and *L. otis orthorhinus*) was found in reasonably heavy forest or as dead material in recently cleared and burned areas. Venezuelan material (*L. plicatus* and *L. tamsianus*) collected by H. B. Baker (1926, pp. 16–21) was all found in heavy forest under logs and debris or in leaf mould near rocky ledges. Living *L. otis orthorhinus* collected in the dry season were found under bark on large logs (young), in leaf litter (young), under hanging bark on a tree trunk six to eight feet above the ground (adults), and under large fallen logs (adult). For a few other species there are brief literature comments concerning the habitat "on ground," "in leaf litter," etc. These are not sufficient, however, to characterize the mainland species as strictly terrestrial. The Puerto Rican species of camaenids show diverse habitats (data from van der Schalie, 1948, pp. 75–83):

Caracolus marginella (Gmelin)—arboreal in plains and foothills;

Caracolus carocolla (Linné)—arboreal in wet forest; among stones or decayed leaves in drier areas;

Polydontes (*Granodomus*) *lima* (Ferussac)—arboreal on whole island, more common in lowlands;

Polydontes (*Parthena*) *acutangula* (Burrow)—arboreal in heavy interior forest, aestivates in bromeliads and leaves in tree;

Polydontes (*Luquillia*) *luquillensis* (Shuttleworth)—arboreal in high rain forest, aestivates in palm bracts and bromeliads;

Zachrysia (*Z.*) *auricoma havanensis* Pilsbry—terrestrial in open, drier areas and in cultivated zones.

It is obvious that the same species (*C. carocolla*) may be terrestrial under some conditions and arboreal under others. Probably the Panamanian *L. otis orthorhinus* is at least partly arboreal during the wet season. The diverse ecology shown by the Puerto Rican species suggests that quite possibly the several species of *Isomeria* with trans-Andean distributions (see pp. 207–208) may be ecologically separated. Certainly ecological studies of the mainland camaenids could yield very interesting and important data.

Gross Anatomy

Very little anatomical information has been recorded in the literature. Moss and Webb (1899) figured part of the genitalia, some radular teeth and the jaw of *Isomeria globosa* (as *I. subcastanea*). H. B. Baker (1926) dissected *L. tamsianus* and *L. plicatus*, figured several aspects of their anatomy and provided a general review of

their morphology. Wurtz (1955), in a supraspecific review of the New World camaenids, added dissections of *L. clappi* and *L. otis orthorhinus* and restudied Baker's material.

Thus only five of the fifty-six species had any anatomical features recorded in literature. Only four species, two of them previously dissected and all represented by very limited material, were available during this study. *Isomeria globosa* (CNHM 70909, two specimens), *L. diminutus* (CNHM 107821, one specimen), *L. unciger* (CNHM 84492, one subadult specimen), and *L. otis orthorhinus* (CNHM, several examples from Panama) were the only preserved specimens located. Only seven species, six *Labyrinthus* and one *Isomeria*, have been dissected and most of these are represented by only one example.

In view of the very limited material, preparation of more than a few comparative notes, following Wurtz (1955) in recognizing systematically important characters, was impossible. Dissections were limited to a review of the radula, jaw, pallial region and genitalia. Following the brief comments on variation in each system, a short discussion covers the possible systematic import of observed variations and suggests a few hypotheses for future testing.

Radula.—In view of the variation in radulae produced by age and diet, data based on single examples are not very reliable. Only a single good radular slide of each species was obtained. The basic tooth data are:

Species	Rows	Tooth formula
Isomeria globosa	179	50–1–50
Labyrinthus unciger	149	37–1–37
L. otis orthorhinus	159+	45–1–51
L. diminutus	197	44–1–44

The asymmetrical formula of *L. o. orthorhinus* was caused by a major deformation in the central region, resulting in grossly distorted denticles. The damage was of long standing, since all current teeth rows showed the same deformities.

Compared with teeth of *L. tamsianus* and *L. plicatus* (see H. B. Baker, 1926, pl. XIV), the cusp structure in *I. globosa* and *L. o. orthorhinus* was almost identical to that described for *L. plicatus*, while *L. unciger* had the structures of *L. tamsianus*. In *L. diminutus* the inner teeth were as in *plicatus*, the outer had more the shape of those in *L. tamsianus*. These are very minor variations and probably are of little or no phyletic significance. It was not thought worthwhile to illustrate the cusp structures.

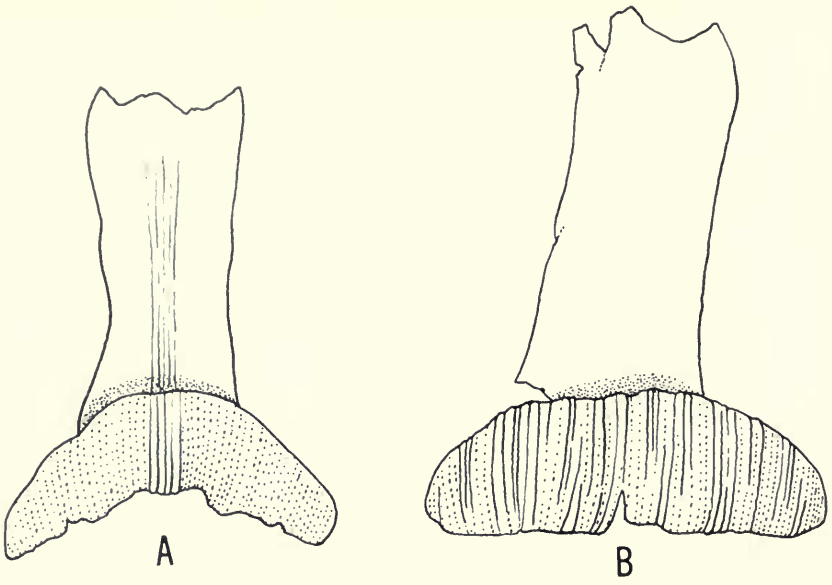


FIG. 1. Jaws of: *a*, *L. unciger*, CNHM 84492; *b*, *L. otis orthorhinus*, CNHM 84495.

Jaw.—Wurtz (1955, p. 109) pointed out that the jaws of most New World camaenids were strongly ribbed, but that in *Caracolus* and *Labyrinthus* the jaws were smooth. Two of the four species I examined had numerous low irregular longitudinal ribs on the jaw. While far from being as prominent as those found in *Polydontes*, the presence of incipient ribs in *Labyrinthus* and *Isomeria* does alter Wurtz's sharp distinction between smooth and ribbed jaws. In *L. unciger* (fig. 1a) the concentric striations representing the edges of the jaw plaits are clearly visible. There are only four or five vague longitudinal wrinkles on the central portion that continue onto the attachment membrane. The lower edge has a relatively prominent central cutting edge. *L. otis orthorhinus* (fig. 1b) has a much thicker, longer, narrower jaw with moderately prominent longitudinal wrinkles over most of the surface. There is no medial protruded cutting edge and the concentric striations are obscured medially, although clearly visible on the outer edges. *L. diminutus* has weak, evenly distributed longitudinal ridges with the concentric ribbing reduced. The lower medial cutting edge is well developed and the shape is much as in *L. unciger*. *I. globosa* has marked concentric striation, but only weak traces of longitudinal ribbing. Shape and form of the jaw are as in *L. unciger*.

Pallial region.—Apparently there is much less variation in the pallial regions of the New World camaenids than is found in the Old World species. Wurtz (1955, pp. 107–109) reviewed the patterns of variation found in the New World forms. *Labyrinthus* was shown to possess a long, narrow kidney that extends about one-half the length of the pallial region and is much longer than wide. Neither the ureter nor the lung surface extends apically from the kidney (K). The pericardium (H) is much shorter than the kidney, and the secondary ureter (KD) is closed to the pneumostome. Dissection of the four available species revealed little variation and confirmed Wurtz's comments.

Distortions are inevitably introduced in straightening out the pallial region for study. Measurements of organ lengths and proportions are thus not very accurate, but despite this still serve to indicate the slight variability in the mainland species.

Species	Pallial length	Kidney length	Ratio of Kidney/ Pallial	Width of Kidney	Ratio of Kidney L/W	Length of Pericardium	Kidney length/ Pericardium
Isomeria globosa	73 mm.	45.5	0.62	2.6–2.9	16–17	11.7	3.9
Labyrinthus unciger	39 mm.	20.0	0.51	1.8	11	5.2	3.9
L. otis orthorhinus	82 mm.	50.5	0.62	2.1–2.6	20–24	10.8	4.7
L. diminutus	52 mm.	27.5	0.53	2.1	13	7.2	3.8
L. plicatus[1]	72 mm.	38.0	0.53	2.9	13	10.0	3.8

[1] Data from Wurtz (1955, pl. 5, fig. 28).

Possibly the larger species will be shown to have a proportionately longer, narrower kidney, but present data are inconclusive. There are no obvious structural differences between the pallial regions of *Isomeria* and *Labyrinthus*, although the West Indian genera (except *Caracolus*) differ markedly in kidney size and proportion.

The structure of the pneumostomal region is quite interesting (fig. 3c). The hindgut (HG) opens separately (A) and a substantial wall of tissue separates it from the pneumono-excretory pore (KX). The secondary ureter (KD) is completely closed to within 1.5 mm. of the outer pneumostomal edge, but then is open ventrally with a double channel developed. The wall of the ureter on one side merges with an inward extension of the mantle collar that is surmounted by a prominent ridge and forms the upper edge of a sharply marked channel leading directly to the exterior. The other wall of the ureter is extended forward and downward at steadily decreasing height until it reaches the mantle collar edge. A "V"-shaped inward extension of the mantle collar forms a ridged barrier dividing the excretory chan-

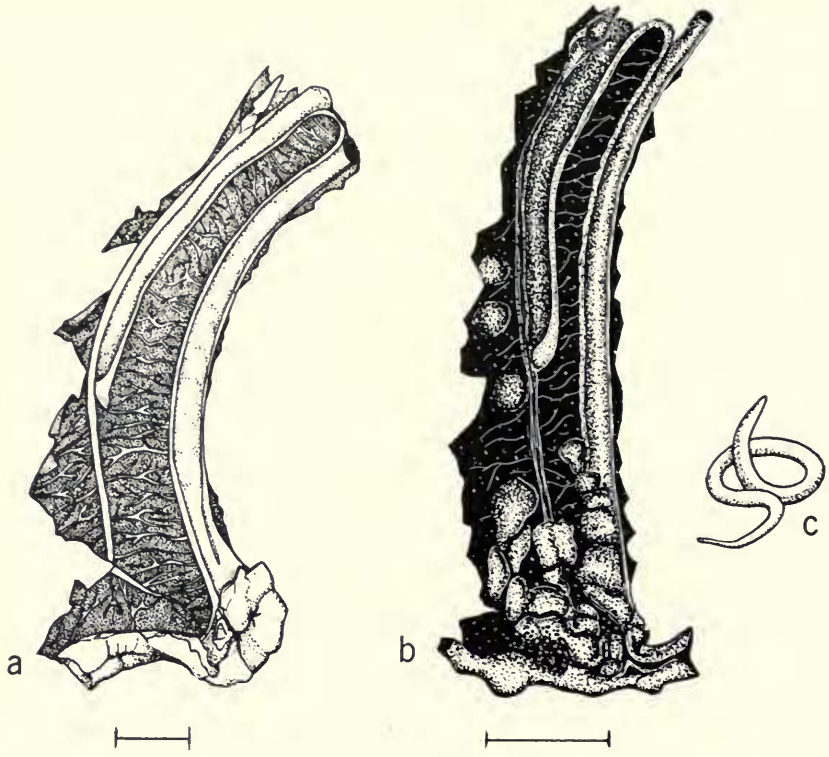


FIG. 2. Pallial regions of: *a*, *L. otis orthorhinus*, CNHM 84495; *b*, *L. diminutus*, CNHM 107821; *c*, encysted nematode from *L. diminutus*. Scale lines equal 10 mm.

nel into two portions, a lower, shallower groove bounded by the thin-walled ureter and an upper deeper groove formed by the mantle collar. The upper groove exits through the pneumostome while the lower groove seems to terminate within the pallial cavity. The functional significance of the lower groove is unknown. It could serve to channel reclaimed water into the pallial reservoir or might serve to bring water from the pallial reserve to flush out the waste products.

Wurtz (1955, pp. 116, 117) reported finding encysted nematodes in *L. clappi* and *L. plicatus*. Three of the four species I dissected were free of large nematode cysts, but *L. diminutus* (fig. 2b) had the anterior pallial region literally choked with quite good-sized cysts. An illustration of the unidentified nematode (fig. 2c) gives an idea of the relatively large size. A few very small cysts were seen in the posterior pallial region of *L. unciger*.

Illustrations (figs. 2, 3) have been presented of the four pallial regions to demonstrate the lack of variability.

Genitalia.—Good descriptions of the genitalia of *L. plicatus* and *L. tamsianus* were given by H. B. Baker (1926, pp. 18, 19, 21). Nothing would be gained by presenting lengthy comments based on

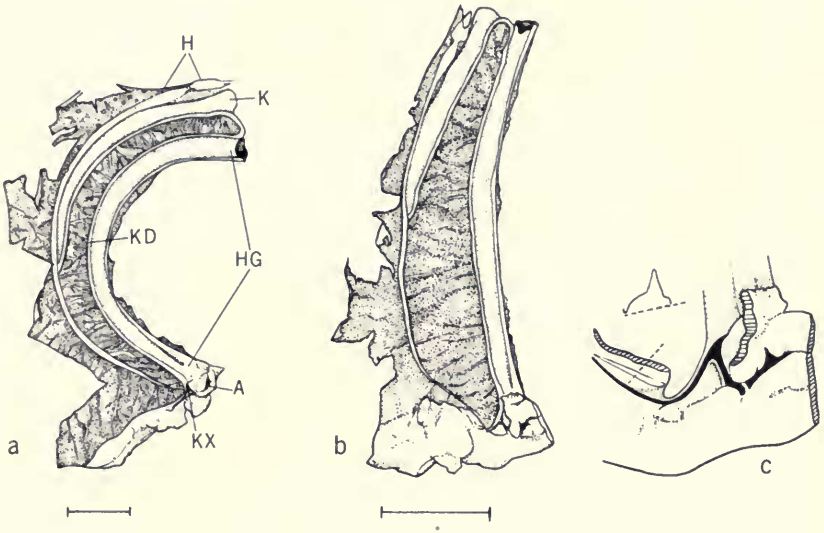


FIG. 3. Pallial regions of: *a*, *I. globosa*, CNHM 70909; *b*, *L. unciger*, CNHM 84492; *c*, *L. unciger*, details of pneumostomal area. Scale lines equal 10 mm.

single specimens, so descriptive comments are limited to comparative remarks. To provide a basis for comparison, a longer descriptive coverage is accorded *L. diminutus*.

L. diminutus (figs. 7, 8)—ovotestis (G) of numerous digitiform, elongate alveoli imbedded in liver, with branched collecting ducts joining to hermaphroditic duct (GD). Ovotestis resembling that of *Pleurodonte* (Wurtz, 1955, pl. 1, fig. 3) much more than that of *L. plicatus* (Wurtz, 1955, pl. 1, fig. 1). Apical portion of hermaphroditic duct straight, becoming strongly sinuated in one plane as it nears the carrefour (X). Just before reaching the carrefour, the duct is sharply reflexed (fig. 7c), giving the appearance of a "talon," then narrowing abruptly before entering the carrefour. Albumen gland (GG) very long and slender, probably caused by seasonal variation. Sacculated uterine oviduct (UT) and prostatic gland (DG) typical of genus. Spermatheca (S) a long, thick sac bound to spermoviduct by connective

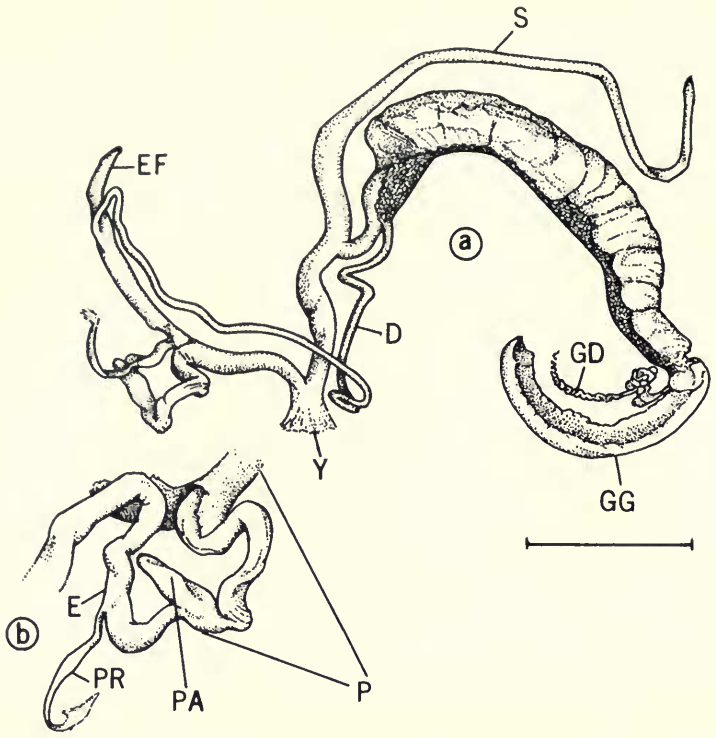


FIG. 4. Genitalia of *I. globosa*, CNHM 70909: *a*, entire system; *b*, detail of penial complex.

tissue, passing beyond aorta and abruptly reflexing anteriorly for a short distance. Vas deferens (D) a narrow tube bound into penioviducal angle, joining the much larger epiphallus (E) at the base of a prominent flagellum (EF). Epiphallus a long slender tube passing into penial sheath and reflexing apically before insertion of penial retractor (PR). Juncture of epiphallus and penis lies about at the next reflexion anteriorly (fig. 7b). Penis (P) widest at apex, tapering rapidly toward atrium (Y). Penial retractor (PR) inserting on diaphragm. Free oviduct (UV) a short, slender tube. Vagina (V) much thicker and quite long. Interior of terminal genitalia diversely sculptured. Lower portion of epiphallus (fig. 8a) with crowded crenulated ridges, becoming larger and more pustulose in the penis and occasionally surmounted by small white denticles (fig. 8b). Vagina with markedly pustulose sculpturing, arranged in a criss-cross pattern, each pustule topped by a hooked denticle.

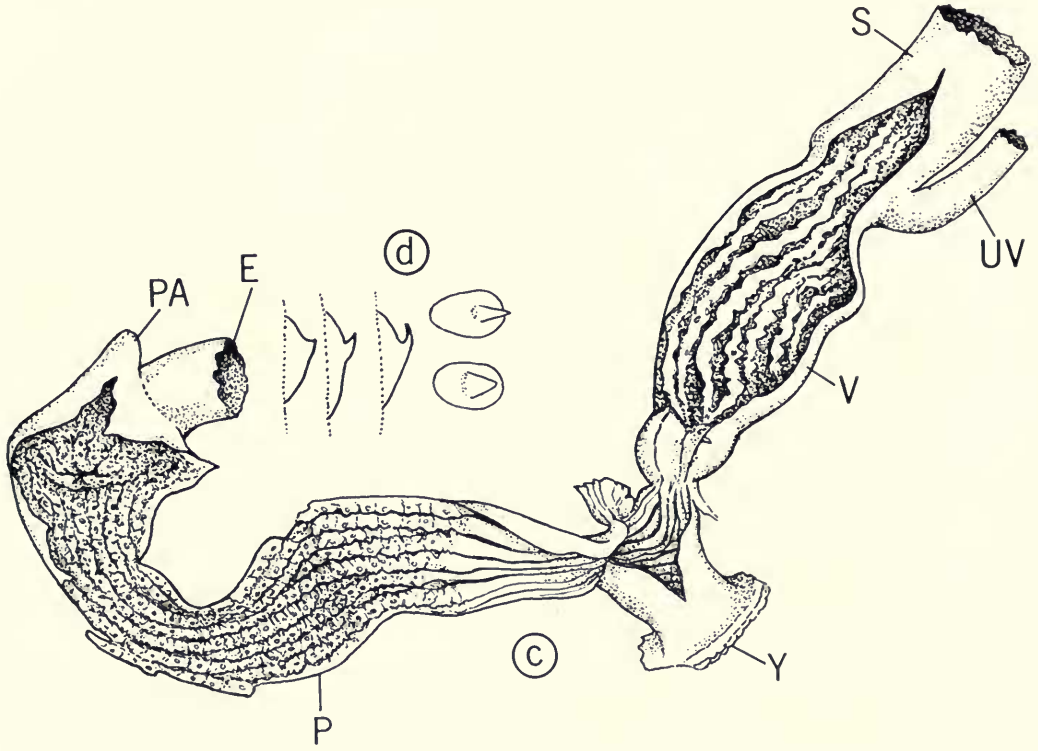


FIG. 4. (*cont.*) Genitalia of *I. globosa*. *c*, internal structure of terminal genitalia; *d*, greatly enlarged view of denticles from inside terminal genitalia. Scale line equals 10 mm.

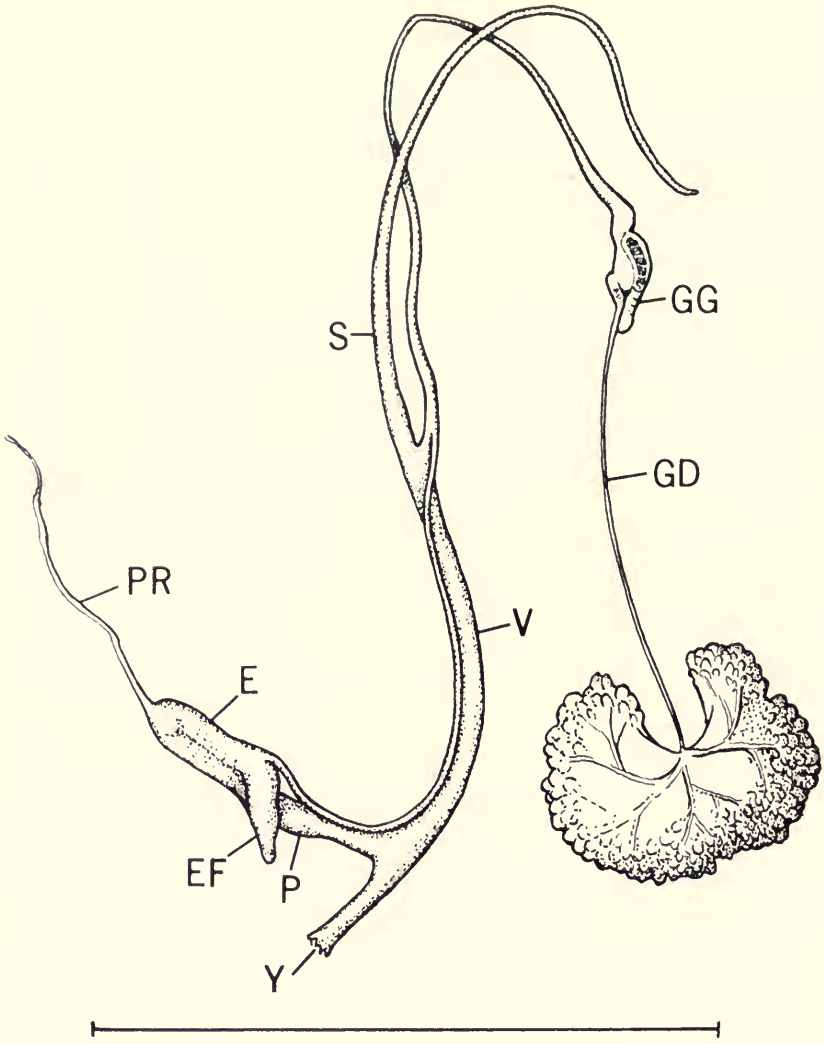


FIG. 5. Genitalia of *L. unciger*, CNHM 84492. A subadult specimen. Scale line equals 10 mm.

The main difference from *L. tamsianus* and *L. plicatus* lies in the greater length of the male genitalia and more pronounced sinuation of the penial complex. The small denticles in the vagina and penis were not found by Baker (1926) or Wurtz (1955) for *L. plicatus*, but are clearly shown by Baker (1926, pl. 13, fig. 70) for *L. tamsianus*. Baker (*loc. cit.*) failed to indicate the reflexion of the spermatheca,

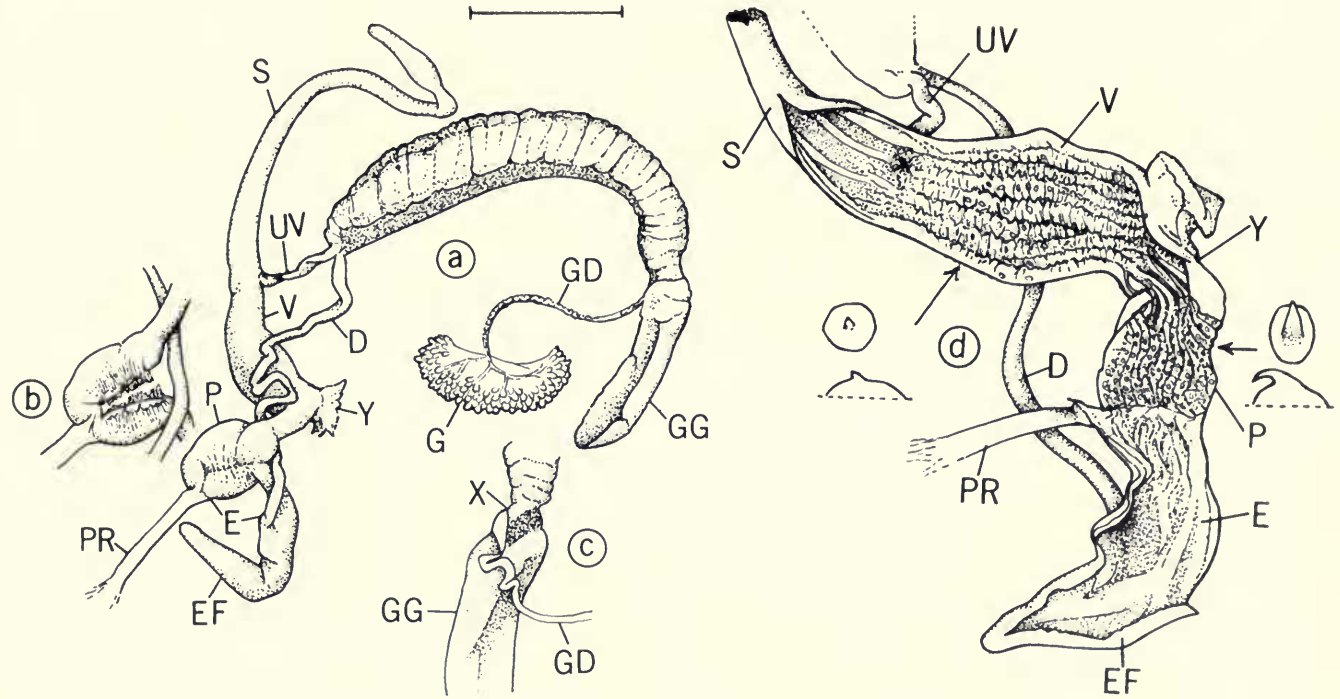


FIG. 6. Genitalia of *L. otis orthorhinus*, CNHM 84495: *a*, entire system; *b*, detail of penial complex; *c*, detail of hermaphroditic duct; *d*, internal structures of terminal genitalia. Scale line equals 10 mm.

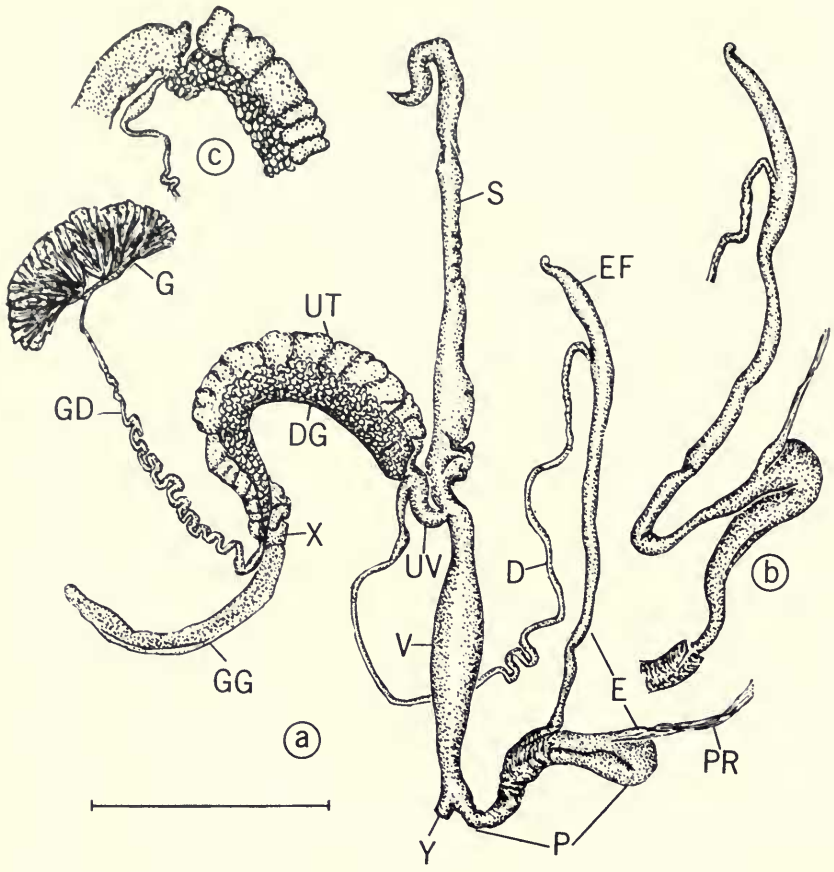


FIG. 7. Genitalia of *L. diminutus*, CNHM 107821: *a*, entire system; *b*, detail of penial complex; *c*, detail of hermaphroditic duct. Scale line equals 10 mm.

but this is properly shown by Wurtz (1955, pl. 5, fig. 25). *L. clappi*, as figured by Wurtz (1955, pl. 4, figs. 20, 21), is very similar to *L. diminutus*, differing only in having a slightly longer penis and epiphallus. *L. diminutus* is thus intermediate between *clappi* and *plicatus* in respect to relative size of the penial complex.

L. unciger (fig. 5)—was represented only by a juvenile example. Meaningful comparisons with other species are thus impossible. The ovotestis was well developed and extended through most of the digestive gland. In contrast, the hermaphroditic duct was a simple tube and the ovisperm duct not yet differentiated into uterine and pros-

tatic portions. Albumen gland was represented by only a few cell-like structures extending apically from base of hermaphroditic duct. Penial complex was more fully developed, with vas deferens, epiphallic flagellum, epiphallus and penis clearly visible. The penial retractor

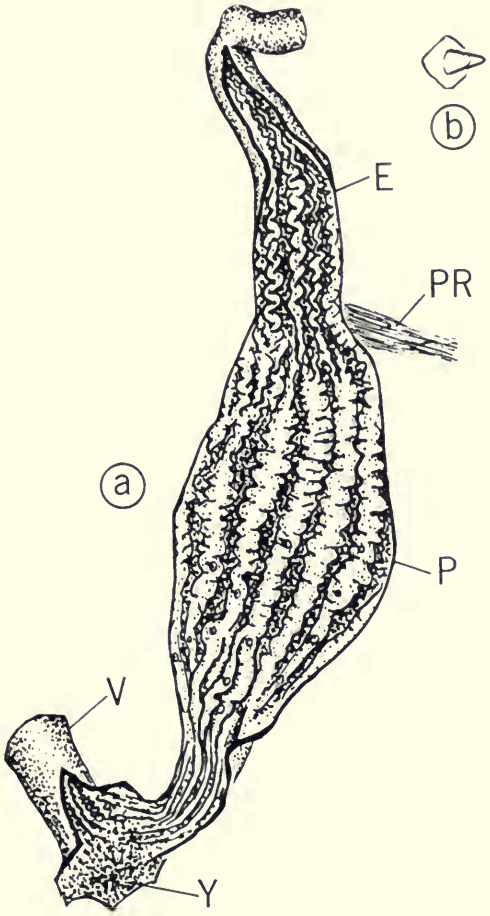


FIG. 8. Interior of penial region in *L. diminutus*: *a*, penis and epiphallus; *b*, denticle form.

was proportionately very long and thin with the penial sheath rather poorly developed.

The extent to which further development would alter the proportionate size of the penial complex is unknown. At its present stage of development, it seems quite similar to the type found in *L. plicatus*.

L. otis orthorhinus (fig. 6)—ovotestis with more ovoid alveoli than in *L. diminutus*. Hermaphroditic duct straight apically, sinuated in a single plane medially, then nearly straight until just before recurved loop (fig. 6c). Albumen gland shorter and thicker than in *L. diminutus*. Free oviduct very slender and appears to insert into the vagina-spermatheca that appears as a single organ. Vagina very thick-walled, spermatheca large and long. Penial complex noticeably shortened into a compact mass. Epiphallic flagellum proportionately very large. Epiphallus shortened, tightly bound to penis by muscular tissue (fig. 6b). Internally, flagellum with large, smooth pilasters, forming smooth to slightly corrugated ridges (fig. 6d) just above insertion of penial retractor. Penis proper very short and bound to epiphallus (fig. 6b), internally with regularly spaced pustulations surmounted by white denticles (fig. 6d) in upper portion, sculpturing changing to smooth ridges near juncture with vagina. Atrium without obvious sculpture. Vagina possessing corrugated ridges with a few denticles, which are distinctly smaller in size and with less prominent hooks than those found in the penis. The spermatheca has only smooth longitudinal ridges.

Wurtz (1955, p. 117) did not find the denticles in his specimens of *L. otis orthorhinus*. Whether this was a result of different preservation or whether they are found only at certain seasons is unknown. Differences in the epiphallic flagellum pilaster pattern (see fig. 6d and compare with Wurtz, 1955, pl. 5, fig. 26) may be artifacts of preservation or the result of individual variations. The most striking feature of the genitalia of *L. otis orthorhinus* is the shortening of the penial organs. The structures are identical with the other species, but the relative size and proportionate width are greatly changed from the elongated species such as *L. clappi*.

Isomeria globosa (fig. 4)—ovotestis as in *L. otis orthorhinus*. Hermaphroditic duct distinctly more strongly convoluted near base, without a separate talon. Spermathecal stalk more slender, vagina shorter and free oviduct slightly larger in diameter. Penial complex of same length as in *plicatus* and *tamsianus*, epiphallus reflexed and bound in penial sheath, penial retractor inserting on epiphallus, penis with a separate flagellum (PA). Interior of penis (fig. 4c) and penial flagellum with denticle-topped corrugated ridges. Basal portion of penis with smooth ridges and lacking denticles. Vagina with crowded corrugated ridges and only a few scattered denticles. The denticles (fig. 4d) are identical to those found in species of *Labyrinthus*. Base of vagina with the same ring of small knobs found in *L. tamsianus*.

The only striking peculiarity of the genitalia is the development of both epiphallic and penial flagellae. These are clearly shown by Moss and Webb (1899). Otherwise the structures do not differ materially from those of the dissected *Labyrinthus*. Generally, the addition of a penial flagellum is not considered to be of any major systematic importance. The other structures are not separable from the variations observed in the few species of *Labyrinthus* dissected.

Discussion.—Only insignificant variations were observed in the radulae, jaws and pallial region. In the genitalia, differences are a matter of proportionate length of the penial organs. Of the six dissected *Labyrinthus*, an attempt to order the species in terms of decreasing length of the penial organs would proceed in the following sequence—*L. clappi*, *L. diminutus*, *L. plicatus*, *L. unciger*, *L. tamsianus* and *L. otis orthorhinus*. The differences are minor between each adjoining pair, although large between the terminal members. The single dissected *Isomeria* shows only one quantitative difference, the presence of a penial appendage. In other characters, it falls within the range of variation shown by the dissected *Labyrinthus*. The ring of knobs at the base of the vagina is also found in *L. tamsianus*.

Even casual studies of the anatomical variety shown by the West Indian camaenids will indicate that the anatomical uniformity of the mainland species is undoubtedly significant. The West Indian genera show great divergence, as do the Old World genera. The apparent lack of any anatomical diversity in South America suggests a very close phyletic relationship. Unquestionably, individuals of the other species groups of *Isomeria* must be dissected before any conclusions can be drawn, but the available anatomical evidence indicates close phyletic ties between the mainland camaenids.

There seem to be no close relationships with any of the West Indian genera. The "hooked" spermatheca, numerous toothed denticles in the penis and vagina, absence of a talon, long vagina, reflexed penis and epiphallus and absence of a penial verge are quite different from the West Indian taxa. Unfortunately, the data on the Old World genera is too fragmentary and scattered to allow comparisons at this time. It may be that they are more closely related to *Chloritis* (*s.l.*) than to any New World genus.

The problem concerning developmental sequence of the denticles in the vagina and penis remains to be solved. Wurtz (1955, p. 115) found the denticles more numerous and more crowded in the penis of *L. clappi* than in the vagina, although well developed in both organs. *L. diminutus* had the vagina with numerous, regularly spaced denti-

cles, but only a few were found in the penis. *L. otis orthorhinus* had many denticles in the penis, but only a few that were reduced in size in the vagina. *I. globosa* had a few scattered denticles in the vagina and many in the penis.

Presumably the denticles serve a stimulatory function. It is well documented that in some groups of land snails an individual acts as a male during one coitus and a female at a succeeding time (or *vice versa*). The denticles may develop first in one organ, degenerate and be reabsorbed after coitus and then grow in the other organ. The collection and study of mating animals will be needed to determine if this postulated sequential arming of the terminal genitalia does occur. It would explain the differences in denticle distribution found in dissected material. Wurtz's failure to observe the denticles in *L. otis orthorhinus* may mean that the denticles are developed only at certain seasons.

At present we know nothing of the mating and reproduction of any camaenid. *Labyrinthus* and *Isomeria* do have these unique denticles in the terminal genitalia, which may serve as functional equivalents of the dart appartus in the Helicidae. Comparative studies between species of *Labyrinthus* and the introduced European Helicidae might yield very interesting and important developmental data.

Classification

The Camaenidae are a rather unspecialized family of helicoid land snails with a disjunctive tropical distribution. Following Wurtz (1955) and Zilch (1960, pp. 596–624), some 37 genera can be recognized. The Old World taxa range from Japan and Korea through the Philippines and Formosa to the New Guinea-Bismarck-Solomon arc and into Australia where a substantial radiation of desert and forest species has occurred, although they do not reach Tasmania. Abundant in Indonesia and southeast Asia, genera (*Traumatophora, Stegodera, Grabauia*) tentatively referred here are found in middle and south China, while several groups extend into parts of India and Ceylon. New World taxa are primarily found on the Greater Antilles, but some *Pleurodonte* reach the Lesser Antilles as far south as Grenada and Barbadoes. Two taxa, *Labyrinthus* and *Isomeria*, have mainland South American distributions.

Knowledge of the anatomy of both Old and New World species is too fragmentary to allow recognition of subfamilies, although Iredale (1937, 1938), in cavalier fashion, has created uncharacterized families for most of the Australian genera. This action should be ignored. Following Wurtz (1955, p. 101), the North American Am-

monitellinae and Oreohelicinae of Pilsbry are considered to be distinct families. A few genera included as Camaeninae by Zilch (*loc. cit.*) should be eliminated. Thus *Polygyratia* Gray, 1847, from Brazil is a Streptaxid (H. B. Baker, 1925) and *Solaropsis* Beck, 1837, found over most of South America and in Eastern Costa Rica is of problematic affinities. Two Old World genera are also incorrectly classified. *Draparnaudia* Montrouzier, 1859, is an Enid (Solem, 1962, pp. 220–223) and *Ariophantopsis* Rensch, 1930, is a dyakiinine Helicarionid (Laidlaw and Solem, 1961, pp. 518, 519).

The most recent review of the classification of the New World taxa (Wurtz, 1955) was based on a multi-character analysis of shell and soft anatomy features. The mainland species were all lumped into *Labyrinthus*, with two subgenera, *Labyrinthus* and *Isomeria*. The latter was divided into the sections *Isomeria* and *Ambages*. Following an earlier historical accident, Wurtz (1955) placed *Labyrinthus clappi* in *Isomeria*. He separated *Isomeria* and *Labyrinthus* on the basis of the elongated penial region and presence of denticles in the penis and vagina in *clappi*, while these structures were absent in the *Labyrinthus* that he studied. Apparently Wurtz (1955) overlooked the dissection of *Isomeria globosa* by Moss and Webb (1899), since no mention was made of this paper.

Pilsbry (1889, pp. 157–159) indicated that *aenigmus* and *vexans* "form a group intermediate between *Isomeria* and *Labyrinthus*," although retaining them in *Isomeria*. Later Gude (1912) proposed the generic name *Ambages* for these and a few species discovered subsequent to Pilsbry's study. Pilsbry had not seen either species, and *L. vexans*, the type of *Ambages*, belongs to the *L. isodon* complex.

My own dissections show that Wurtz's distinctions are untenable, since the denticles occur in *Labyrinthus* and the genitalia of *L. diminutus* bridge the gap between *clappi* and the species dissected by Wurtz. The only *Isomeria* that has been dissected, *I. globosa*, does have a penial appendage that is absent from the studied *Labyrinthus*. This is not usually a character of generic importance, and the other anatomical features do not show important differences from *Labyrinthus*. Only one-eighth of the 56 species from the mainland have been dissected and only one of the 28 placed in *Isomeria*. On the basis of anatomy, there is no justification for generic separation.

Nevertheless, since the 1850's it has been recognized that the mainland species fall into two groupings: a lowland to medium elevation series with heavier occlusion of the aperture (*Labyrinthus*), and a high mountain series with very small to vestigial teeth in the aperture (*Isomeria*). With the exception of two species described

below, *I. inexpectata* and *I. minuta*, the division into *Labyrinthus* and *Isomeria* is reasonably simple. *I. minuta* has the basal and lower palatal teeth of a *Labyrinthus*, but lacks a parietal lamella, while *I. inexpectata* has the shape of *Isomeria*, but a reduced form of *Labyrinthus*-type dentition.

The available anatomical evidence demonstrates a close affinity between the dissected species, but the combination of altitudinal and conchological distinctions warrants taxonomic recognition. Thus two genera, *Labyrinthus* and *Isomeria*, are considered here. While recognizing the differences in shell aperture and altitudinal range, the distinction may have no phyletic significance. We have no knowledge of the ecological niches of *Isomeria* and *Labyrinthus*. If they prove to be different, then a monophyletic origin for each group would be possible. If their ecological positions overlap, then a polyphyletic origin of *Isomeria* from *Labyrinthus* (or *vice versa*) would seem more likely. In view of the diverse apertural structures of the shells, I would incline toward a polyphyletic origin of the two conchological types. Present data are totally insufficient to resolve the problems, and a division into two genera serves a practical purpose in recognizing shell form and altitudinal zonation.

Fossil Record

No fossil camaenids have been reported from the South American mainland. A Jamaican Miocene fossil (*Pleurodonte bowdeniana* Simpson, 1894) is known from two fragments (Simpson, 1894, p. 450, pl. 16, figs. 3–5). To a certain extent it resembles the Ecuadorean *Isomeria globosa* form *kobeltiana*. Both have a closed umbilicus and no parietal lamella, but have a prominent, posteriorly indented lower palatal tooth and a basal tooth. The fossil has a much larger basal tooth and the lower palatal tooth seems to be wider and flattened above. The similarities are almost certainly convergent.

Several species from the Lower Miocene Silex beds of Tampa, Florida (see Dall, 1915, pp. 23, 24, pls. 1, 2, 4) have been placed in *Pleurodonte*, but with their own subgenus, *Pleurodontites* Pilsbry, 1939. None shows great similarities to any of the species considered here. Other North American camaenid fossils are dubiously referred to the family or are based on unlocalized, unstratified material (*Hodopoeus crassus* Pilsbry and Cockerell, 1945).

The very fragmentary, scattered fossils provide no helpful data concerning the origins or distributions of the New World camaenids. The only fact revealed is that camaenids were formerly present in Florida but are now absent from North America.

SYSTEMATIC REVIEW

Genus **LABYRINTHUS** Beck, 1837

(=*Lyrostoma* and *Lyriostoma* Swainson, 1840, *Ambages* Gude, 1912) Index Molluscorum, p. 33.

Type species.—*Helix otis* Lightfoot, 1786 (=*Helix labyrinthus* "Chemnitz" Deshayes, 1838) by subsequent designation of Herrmannsen (1846, p. 569).

Range.—Northern Costa Rica south to Madre de Dios, Peru, east to Caracas, Venezuela and the confluence of the Rio Tapajóz and Amazon in Pará, Brazil. Apparently absent from the Pacific slopes of the Andes below the Calima River basin in Valle de Cauca, Colombia, except for three records from the upper Rio Esmereldas drainage of Ecuador. Found from near sea level to a maximum recorded altitude of 7,000 feet elevation.

Diagnosis.—Shell small to large (diameter 12.5–60 mm.); depressed globose to planulate; surface sculpture of growth wrinkles or granulations, but never ribbed; spire nearly flat to moderately elevated; periphery rarely rounded, usually acutely angulated or protrudingly keeled; umbilicus partly (rarely completely) closed by extension of basal and parietal lips; aperture strongly deflected near end of body whorl, partially obstructed in adult by gross expansion of lips and development of various denticles and lamellae; parietal lip raised and with reflected edge (except *L. sieversi* and *L. clappi*), basal and palatal lips thickened and strongly reflected, all lips varying from straight to strongly indented or sinuated; parietal wall with single short to long, curved to sinuated lamella (bifid in *L. sharmani*) that stops short of or variously merges with the elevated parietal lip; basal lip straight to sinuated, normally with one lamellar knob marking its outer boundary (absent in *L. aenigmus*), occasionally with a second inner knob; lower palatal lip with single crescentic lamella, hooked lamellar tooth, large transverse lamellar plate or "Y"-shaped bifid tooth with a deep indentation behind lip; upper palatal lip with weak lamella or triangular knob in a few species. Soft parts with typical camaenid structures, distinguished primarily by the elongated, sau-

sage-shaped kidney; ovoid to digitiform alveoli in the ovotestis; absence of a talon, verge or accessory penial organs other than a flagellum; presence of a long, recurved spermathecal duct; smooth to weakly ribbed jaw; and presence of white, calcareous denticles topping the longitudinal ridges and pustules of the vagina and penis during at least part of the life history.

Remarks.—Variously placed as a subgenus or section of *Caracolus*, *Lucerna*, *Helix* or *Pleurodonte* in the 19th century, *Labyrinthus* always has been recognized as a discrete group of species confined to mainland America. The shell is differentiated from that of *Isomeria* in having the aperture greatly narrowed by large folds and lamellae.

The function of the apertural folds is unknown. They do not develop until the animal stops increasing the shell diameter and forms the "adult" lip. Quite probably the animal is sexually mature before formation of the lip, although a specimen of *L. unciger* with partly formed lip had quite juvenile genitalia (fig. 5). Pilsbry (1889, p. 159) and von Martens (1892, pp. 175, 176) speculated that the apertural folds might provide protection against snail-eating carabid beetles, but there is no evidence concerning possible beetle predation. On rare occasions the coati has been observed to eat *L. otis orthorhinus* (see p. 112), but we have no other information on the use of *Labyrinthus* for food by animals or man. The apertural folds are very effective in narrowing the aperture of the adult, but whether this affects predation is unknown.

The presence of apertural armature is a common phenomenon in land snails and has evolved separately in many and diverse families. For example, the teeth may appear at or soon after hatching (Tornatellinidae, Strobilopsidae, Endodontidae) and persist throughout life; in others (some Zonitidae and Enidae) there are teeth in the young, but none in the adults; while in many families (Pupillidae, Polygyridae, Odontostominae and Camaenidae) the teeth appear only when the reflected lip is formed and further increase in shell size ceases. Every conceivable type of variation is known and the character of the teeth and time of formation can vary within a family. Several somewhat divergent systems of nomenclature are in use for apertural armature. In view of the varying shape of the apertures and independent origins of the teeth, no attempt at standardization of terminology seems necessary or desirable.

Previous descriptions of the apertural folds in *Labyrinthus* have been very general, complicating problems of identification and comparison. For convenience in working with this group, a simple divi-

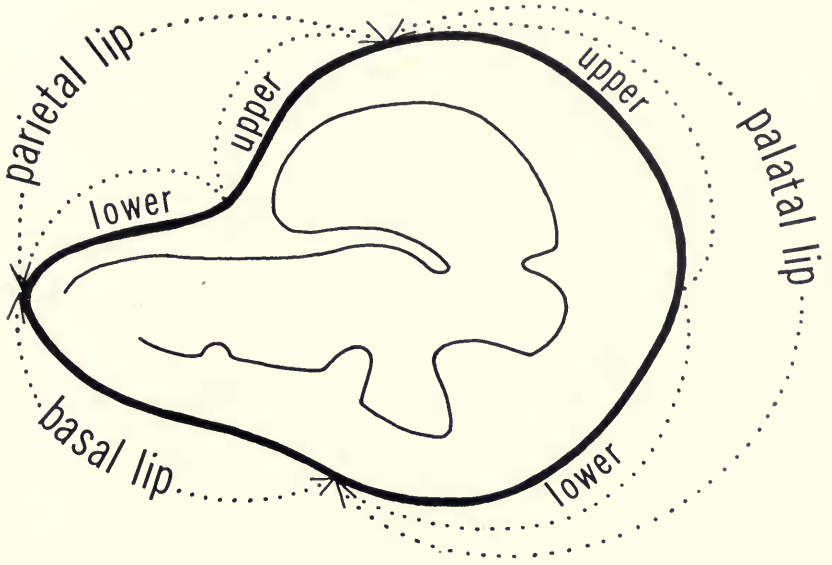


FIG. 9. Apertural zones in *Labyrinthus*.

sion of the aperture into three zones is proposed (fig. 9). The areas are delineated as:

PARIETAL LIP—portion of raised lip (or callus edge) fastened to penultimate whorl

Lower Parietal Lip—portion from junction of the parietal lamella to basal lip

Upper Parietal Lip—portion from junction with parietal lamella to junction with upper palatal lip

PALATAL LIP—portion of lip bordering body whorl from edge of parietal lip to outer edge of basal tooth

Upper Palatal Lip—portion of lip between parietal wall and periphery of body wall

Lower Palatal Lip—portion of lip from periphery of body whorl to inner edge of basal tooth

BASAL LIP—portion of lip from outer edge of basal tooth to junction with parietal lip

In forms where the parietal lamella does not reach or merge with the parietal lip, a division into upper and lower parietal lips is not possible. The relative size of the two parietal lip divisions varies with

the type and point of union of the lamella and lip. The nearly constant presence of a prominent basal tooth (except in *L. aenigmus*) and usual presence of a marked sinuosity at that point in the aperture make the basal tooth a convenient boundary between basal and palatal lips.

In most groups of snails with apertural dentition (*i.e.*, Pupillidae, Endodontidae, etc.) the aperture is divided into parietal, columellar, basal and palatal zones. The columellar region is a short zone forming the side of the umbilicus and extends from the parietal wall to the curve of the lip marking the baso-columellar angle. This zone is prominent in shells with vertical or only moderately deflected apertures. In *Labyrinthus* the extreme deflection of the aperture and tendency of the reflected lip to partly cover or dip into the umbilicus (see figs. 19f, 21a) has reduced the "columellar region" to the actual curve connecting the basal and parietal lips. This area is minimal in size, has no dentition and cannot be delineated from the basal and parietal areas. While technically it would be proper to call this curve the columellar region, practically this is of no importance in *Labyrinthus* and the term "columellar area" is not utilized in this study.

Each of the three zones shows moderately extensive variations. In two species with completely closed umbilicus, *L. sieversi* and *L. clappi*, the parietal lip is not elevated, but a very heavy callus covers the parietal region. In *L.* sp., also with a closed umbilicus, the lip is only moderately raised, and in *L. aenigmus*, where the lips cover most of the umbilicus, the elevation of the parietal lip is greatly reduced. Most species have the parietal lip simply curved, but in those species in which the parietal lamella merges with the parietal lip, the latter may be grossly distorted with the upper portion greatly reduced in prominence. The series of transitions to this are discussed under the *L. isodon* group, and reaches its highest development in *L. magdalenensis*, new species, and *L. otostomus* of the *aenigmus* complex. All species have a parietal lamella, which is the largest tooth in forms where it merges with the parietal lip, but is much less prominent in species where there is no such junction.

The basal lip is occasionally straight (*L. tamsianus*, for example) and then varies to the highly sinuated condition seen in *L. subplanatus sipunculatus*. In every species except *L. aenigmus*, the basal-palatal lip margin is marked by a high conical or lamellar tooth. In a few species a small to prominent second, inner basal tooth has developed. Considerable variability is shown in the extent to which the parietal and basal lips parallel each other before dipping into the

umbilical opening (see figs. 30, 32, 36) and the extent to which they do dip into the umbilicus.

The lower palatal region shows variously constructed teeth. The simplest condition, characteristic of most members of the *isodon* complex, is a single crescentic lamella situated at the lip edge and generally perpendicular to the body wall at that point. From this, several specializations have developed. In a group characteristic of the Upper Amazonian basin (*L. raimondii* complex) the crescentic lamella is supplemented by a conically triangular tooth twisted upward (see fig. 21) and the two are joined by a high ridge forming a "Y"-shaped structure. A deep posterior indention behind the lip marks the area of the ridge and does not require a thick calcium deposit underneath these teeth. Some members of the *isodon* complex (*L. dunkeri* and *L. magdalenensis*) have two crescentic lamellae on the lower palatal lip and in *L. otostomus* there are two parallel crescentic lamellae connected by a ridge with posterior indention. The other two types of structure are quite distinctive. In the *L. unciger* complex the lower palatal wall has a long entering ridge or lamella (whose edge may be smooth or fluted) surmounted posteriorly by a recessed "T"-shaped lamella or "fish-hook" structure (see fig. 29). In the *L. otis* series, the lower palatal lamella has become *transversely* oriented and varies from a conical ridge (*L. marmatensis*, fig. 36e) to a huge, spade-shaped crescent that almost touches the parietal lamella (*L. otis*, *L. subplanatus*, figs. 30, 32).

In the carinated or keeled species, the boundary between the upper and lower palatal lips is marked outside the aperture by the periphery and inside only by an angle. In some species the periphery has a distinct groove inside the aperture and in *L. subplanatus* the peripheral groove is reflected, or even turned upward to form a spout (fig. 35). Comparatively few species have dentition on the upper palatal wall. Generally it is in the form of a small conical or crescentic lamella, but *L. magdalenensis* has a lamellar ridge and there is usually a deeply recessed small tooth located above the top of the lower palatal tooth in the *L. otis* complex.

There is also considerable variability between species in the degree to which the aperture is deflected. Because of the sinuated lip and lack of any accurate way to measure the exact degree of deflection, no attempt has been made to utilize this as a systematic character. Generally, apertural deflection is cited as the number of degrees of inclination from the shell axis. In species with grossly deflected lips, aligning of the shell axis becomes purely guesswork.

Variability in spire outline and point where the deflection starts make it impossible to utilize the sutural line as a point of standard reference. Similarly, the sinuated nature of the lip also renders the taking of standard measurements extremely difficult. The side views of the apertures and spires serve to indicate the general degree of deflection and partially compensate for the lack of quantification.

Identifications can be made primarily from the apertural armature, although variations in size, form, degree of carination of the periphery, umbilical width, height and outline of spire, color pattern and surface sculpture are quite marked. Juvenile shells, which lack any trace of lip armature, can be identified only by comparison of their apical whorls, sculpture, color and whorl increment with adult specimens.

Classification of *Labyrinthus*

In view of the limited number of species dissected and the paucity of well localized material, it is premature to attempt anything more than a grouping of species. Certain relationships are obvious. *L. unciger* and *L. creveauxianus* form a natural pair; *L. otis, L. subplanatus, L. plicatus* and *L. marmatensis* agree in form, basic apertural characters and show a cohesive pattern of distribution; many forms grouped around *L. raimondii* show a bewildering variety of minor variations; and stages in the development of merging of the parietal lip and lamella can be seen in species related to *L. leucodon, L. isodon, L. manueli, L. vexans* and *L. magdalenensis* with *L. otostomus* an obvious derivative.

Two possibly unwarranted working assumptions have been made in recognizing five species groups of unequal value. Small size and simplicity in apertural armature may have preceded large size and complexity in apertural armature. Immediate and obvious exceptions are the small lowland *L. tamsianus* whose reduced apertural characters may have been derived from those of the larger, upland *L. leucodon*, and the reduced dentition of the Venezuelan *L. plicatus* when compared with the smaller *L. subplanatus*. As a general rule, however, comparison of probably related species shows increasing complexity of tooth structure with increasing size. Secondly, it is assumed that the apertural characters are more stable than differences in form, size, coloration or degree of peripheral angulation. Groupings based on apertural structures show rather definite geographical patterns and accommodate most of the species in fairly clear cut groups.

Three species groups are easily and adequately defined: group of *L. unciger* by the recessed, hooked or "T"-shaped lower palatal lamella; group of *L. otis* by its transversely oriented lower palatal tooth; and group of *L. raimondii* by its "Y"-shaped, bifurcated lower palatal tooth. The group of *L. isodon* is less cohesive, having simple crescentic lamella(e) on the lower palatal wall, but a series of modifications in the relationship of the parietal lamella and lip that lead toward the structures found in the *L. aenigmus* group. *L. magdalenensis* and *L. dunkeri*, in particular, seem somewhat distinct from the rest of the *L. isodon* type, having several extra denticles and not fully conforming with the others in tooth structure. Particularly difficult are the relationships of the two species from the Sierra Nevada de Santa Marta in Colombia, *L. sieversi* and *L. clappi*. Both have the umbilicus completely closed and the parietal lip is not elevated, but has been replaced by a heavy parietal callus. *L. sieversi* has the bifurcated lower palatal tooth of the *L. raimondii* series, and, for convenience, has been grouped with them, although geographically isolated. *L. clappi* has simple but grossly thickened teeth. Because of a general resemblance in form, size and thickening of the teeth it has been grouped with *L. aenigmus* and *L. otostomus*. The latter three probably represent separate derivations from the *isodon* group, which is tentatively considered the least specialized of the species groups. Available data is insufficient to suggest derivation or interrelationships of the other groups.

KEY TO THE GROUPS OF *LABYRINTHUS*

1. Lower palatal wall with a deeply recessed, hooked or "T"-shaped lamella. Group of *Labyrinthus unciger*

   Lower palatal wall variously armed with teeth or lamellae situated on lip....2

2. Lower palatal wall with a high conical or spade-shaped transverse lamella. Group of *Labyrinthus otis*

   Lower palatal wall with one or more crescentic lamella that are not transversely placed.....3

3. Two lower palatal teeth, upper triangular, lower crescentic, connected by a high callus, forming a "Y"-shaped structure, shell unicolored or with lighter peripheral zone.....Group of *Labyrinthus raimondii*

   One lower palatal tooth, or with two crescentic lower palatal teeth and either two basal or an upper palatal tooth present, or lower palatal teeth as above, but shell yellow-brown with spiral red bands.....4

4. Diameter more than 35 mm., or umbilicus completely closed, or with a triangular ridge at lower edge of upper palatal lip forming a peripheral groove with parallel lower palatal teeth (fig. 23a).....Group of *Labyrinthus aenigmus*

   Diameter less than 32 mm., umbilicus distinctly open, upper palatal tooth (when present) not forming edge to a peripheral groove. Group of *Labyrinthus isodon*

Keys to the species are given for each group. Data relating to zoogeography, zonation and possible geographic trends follows the account of the species.

REVIEW OF THE SPECIES

Group of *Labyrinthus isodon*

A series of minor and confusing differences prevent any simple characterization of this group. Most specimens range from 17 to 25 mm. in maximum diameter, although individuals of *L. magdalenensis* new species are slightly larger, *L. manueli* (Higgins) reaches a maximum of 30 mm., *L. quadridentatus* (Broderip) is smaller and the dwarf *L. tamsianus* (Dunker) ranges down to 12.5 mm. The umbilicus is always partly open. Spire elevation and shape ranges from depressed globose to almost planulate. Most species are unicolored, but *L. magdalenensis* has a brilliant speckled pattern, and *L. dunkeri* spiral reddish bands on a lighter background.

Only *L. tamsianus* has been dissected (H. B. Baker, 1926). Its anatomy shows only minor differences from that of *L. plicatus* (Born). No soft parts were available during this study, and classification had to be based on differences in the apertural dentition. Most of the species seem to be closely related, but *L. dunkeri*, in particular, seems rather different.

There is considerable variability in the apertural teeth. Perhaps the most fundamental changes are in the relationship of the parietal lamella and the parietal lip. Generally, a distinctly elevated parietal lip is formed at adulthood. Its origin may lie in the narrow parietal callus edge found in *Isomeria*. In most *Labyrinthus* this ridge has been altered to an extension of the body wall with a slightly to strongly reflected lip edge. Only in *L. sieversi* and *L. clappi*, with their totally closed umbilici, are the parietal walls with only a heavy broad callus. This may be a secondary reduction associated with umbilical closure. The simplest condition of the parietal lamella is a high, curved blade that is rather short and whose anterior end lies distinctly short of the raised parietal lip. This condition is typical of the *raimondii* and *unciger* series as well as being found in *L. triplicatus* and *L. quadridentatus* (see figs. 10, 21, 28). *L. sieversi* has no elevated parietal lip, which may account for the form of the parietal tooth in that species as well as in *L. clappi*. Although *L. tamsianus* has the same short parietal lamella, it is suspected that this is a secondary development through reduction of the type of dentition found in *L. leucodon* (see figs. 12, 13).

Actual union of the parietal lamella and lip has taken two forms. In one series a sinuately twisted bladelike lamella gradually is lengthened and finally inserts perpendicularly into the lip. The short lamella in *L. dunkeri* (fig. 14a) is also found in the *unciger* group and in moderately lengthened form in some of the *plicatus* series. Finally, in the *raimondii* series, *L. ellipsostomus* (fig. 18) has the lamella stop just short of the parietal lip and in *L. leprieurii* the lamella inserts perpendicularly into the lip (fig. 16).

In the other series, leading from the *isodon* to the *aenigmus* complex, the parietal lamella joins or merges with the lower parietal lip at an extreme angle, often with the upper part of the parietal lip greatly reduced in prominence. Some of the *plicatus* series show the same type of joining. *L. leucodon* (fig. 12b) has the simplest form of union, with the parietal lamella beginning to decrease in height just before joining the lip and the upper part of the lip not appreciably reduced in size. In *L. leucodon umbrus* (fig. 12c), the parietal lamella has not started to descend before the union. This type of tooth is easily derivable from the simple curved blade found in *L. triplicatus*. A further development is seen in *L. isodon* (fig. 14b) where the lip and lamella join at a distinct angle, but the upper portion of the parietal lip is greatly reduced in height. *L. manueli* (fig. 14d) and *L. vexans* (fig. 14c) are very similar, except that the merging of the lamella and lip is not marked by a distinct angle. A further modification occurs in *L. magdalenensis* (fig. 10d) in which the highest part of both lamella and lip is at the point of merging, with the upper parietal lip greatly reduced in size and the lower parietal lip and lamella decreasing in height from the point of union. The several members of the *aenigmus* series have basically the same type of union of parietal lip and lamella.

There is much less variation in the basal lip dentition. All species have a rounded knob or crescentic lamella marking the junction of the basal and lower palatal lips. Some individuals of *L. manueli* may have a second low knob, while a distinct inner tooth is found in *L. isodon* and *L. quadridentatus*. *L. dunkeri* is unique in having a diagonal inner lamella (fig. 14a) for the second tooth.

The lower palatal wall is variously armed. *L. triplicatus* and *L. quadridentatus* have a spade-shaped lamella that differs from the crescentic lamella of *L. leucodon*, *L. vexans*, *L. manueli* and *L. tamsianus* only in being proportionately narrower. Conceivably, this is a forerunner of the huge transverse tooth found in the *plicatus* series. *L. magdalenensis* (fig. 10d) has two widely separated crescentic la-

mellae, the upper just below the periphery. *L. dunkeri* has a lower crescentic lamella and a small upward twisted triangular tooth that is connected by a weakly elevated ridge with a corresponding indentation behind the lip. This is very close to the situation in the *raimondii* series.

Few species have significant upper palatal dentition. A small triangular knob in *L. leucodon* and *L. tamsianus*, low diagonal lamellae in *L. dunkeri* and *L. magdalenensis*, and a crescentic lamella located on the periphery in *L. isodon* and slightly above in *L. vexans* are the only known examples.

Distributional information (see fig. 57) is fragmentary and the scattered ranges emphasize the diverse nature of this grouping. *L. triplicatus* and *L. quadridentatus* are closely allied species of Western Panama and Costa Rica. *L. vexans* has been reported from Frontino and Cañasgordas, Antioquia, Colombia. No others are known until *L. dunkeri*, *L. magdalenensis* and *L. isodon* in the Sierra de Perijá along the Colombian–Venezuelan border. *L. dunkeri* has been recorded from old museum collections as occurring in the Cordillera Occidental and Cordillera Central of Antioquia, Colombia, but these records may not be valid. *Labyrinthus leucodon* is known from Cordillera Mérida of Venezuela, and both *L. leucodon* and *L. tamsianus* live in the coastal ranges of Central Venezuela. They are a closely allied pair of species, probably equivalent to the *quadridentatus-triplicatus* pair of Costa Rica and Panama. No species of this group have been reported from the Andean region of Southern Colombia. *L. manueli* is fairly widely distributed in the Ecuadorean Andes. Its upper known range is 2,000 feet, but it may be found at higher elevations. The lower limit is uncertain, but may be around 300 to 1,000 feet.

KEY TO THE *LABYRINTHUS ISODON* COMPLEX

1. Parietal lamella at least slightly separated from parietal lip.....2
   Parietal lamella reaching or fusing with parietal lip.....6
2. Shell unicolored or with a lighter peripheral band.....3
   Shell with reddish spiral bands on a lighter background.
   Labyrinthus dunkeri (Pfeiffer, 1852)
3. Periphery angulated, but not acutely carinated; Costa Rica and western Panama.....4
   Periphery acutely carinated, teeth small; Venezuela.
   Labyrinthus tamsianus (Dunker, 1847)
4. Two basal teeth, diameter less than 21 mm.; Pacific drainage.....5
   One basal tooth, diameter more than 22 mm.; Atlantic drainage.
   Labyrinthus triplicatus (Martens, 1868)

5. Periphery sharply carinated, diameter less than 19 mm.; Golfo Dulce, Costa Rica and Comarca de Baru, Panama.
Labyrinthus quadridentatus quadridentatus (Broderip, 1832)
Periphery obtusely angulated, diameter more than 19 mm.; San José and Cartago, Costa Rica.... *Labyrinthus quadridentatus biolleyi* new subspecies

6. One lower palatal tooth.....7
Two lower palatal teeth.....*Labyrinthus magdalenensis* new species

7. Basal lip with one tooth present.....8
Basal lip with two teeth present.....11

8. Upper parietal lip much lower than parietal lamella.....9
Upper parietal lip equal in height to parietal lamella.....10

9. Upper palatal tooth absent; Ecuador....*Labyrinthus manueli* Higgins, 1872
Upper palatal tooth present; Antioquia, Colombia.
Labyrinthus vexans (Dohrn, 1875)

10. Umbilicus more than half covered by extension of basal and parietal lips; teeth large and heavy; Aragua, Venezuela.
Labyrinthus leucodon umbrus Thompson, 1957
Umbilicus less than half covered by extension of basal and parietal lips; teeth relatively small; Mérida to Yaracuy, Venezuela.
Labyrinthus leucodon leucodon (Pfeiffer, 1847)

11. Upper palatal tooth present.....*Labyrinthus isodon* (Pfeiffer, 1853)
Upper palatal tooth absent.....*Labyrinthus manueli* Higgins, 1872

Labyrinthus triplicatus (von Martens, 1868). Figures 10a, 11a.

Helix triplicata von Martens, 1868, Malak. Blätt., **15**, p. 156—Costa Rica (Carmiol!); Pfeiffer, 1869, Novit. Conch., **3**, pp. 460–461, pl. 101, figs. 1–3; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 463.

Helix aesopus Angas, 1878, Proc. Zool. Soc. London, **1878**, pp. 72–73, pl. 5, figs. 11–12—Buena Vista (?Alajuela), Costa Rica at 3,000 feet elevation (Boucard!); Angas, 1879, *loc. cit.*, **1879**, p. 476—coast region and hills of Urén to 3,000 feet elevation (Gabb!).

Helix (*Labyrinthus*) *triplicata* (von Martens), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 165–166, pl. 41, figs. 17–19; Kobelt, 1894, Syst. Conch. Cab., I (12), **4**, pp. 629–630, pl. 180, figs. 14–15.

Helix (*Labyrinthus*) *triplicata* var. *aesopa* (Angas), Pilsbry, 1889, Man. Conch. (2), **5**, p. 166, pl. 64, figs. 27–28.

Labyrinthus triplicatus (von Martens), von Martens, 1892, Biol. Centr. Amer., Moll., p. 176, pl. 10, figs. 2, a–c; Biolley, 1897, Molluscos terr. fluv. meseta central Costa Rica, p. 11—Sarapiquí, Costa Rica at 500 meters elevation (Biolley!); von Martens, 1901, Biol. Centr. Amer., Moll., p. 628.

Pleurodonte (*Labyrinthus*) *triplicatus* (von Martens), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95.

Pleurodonte (*Labyrinthus*) *aesopus* (Angas), Pilsbry, 1926, Proc. Acad. Nat. Sci., Philadelphia, **78**, p. 127—Cahuita and Talamanca Valley, Costa Rica.

Range.—Costa Rica, from coastal areas of Limón to possibly 4,500 feet in elevation as far north as Sarapiquí, Heredía and Buenavista, Alajuela. Possibly in Bocas del Toro, Panama.

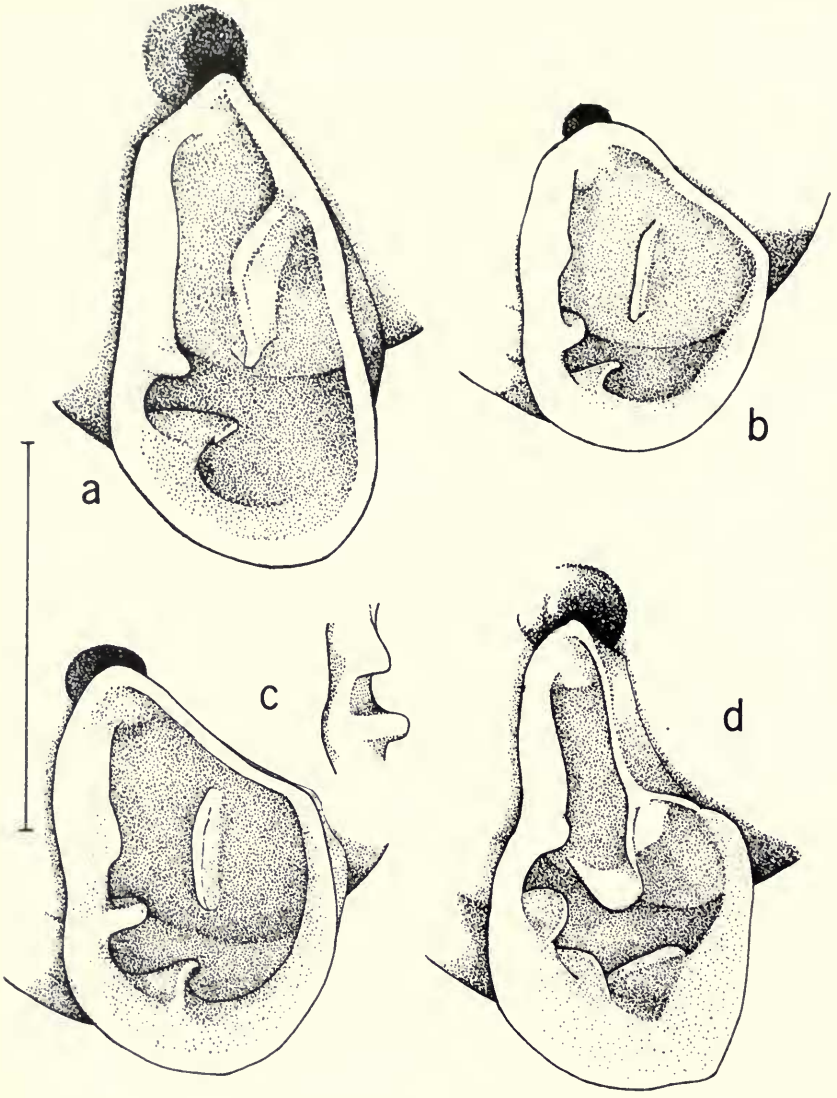


FIG. 10. Apertures of: *a*, *Labyrinthus triplicatus*, Navarro, Costa Rica, CNHM 63776; *b*, *Labyrinthus q. quadridentatus*, Coto, Costa Rica, USNM 532569; *c*, *Labyrinthus q. biolleyi*, Guaitil de Pirris, Costa Rica, CM 62.5755. Holotype; *d*, *Labyrinthus magdalenensis*, Tierra Nueva, Magdalena, Colombia, USNM 533878. Holotype. Scale line equals 10 mm.

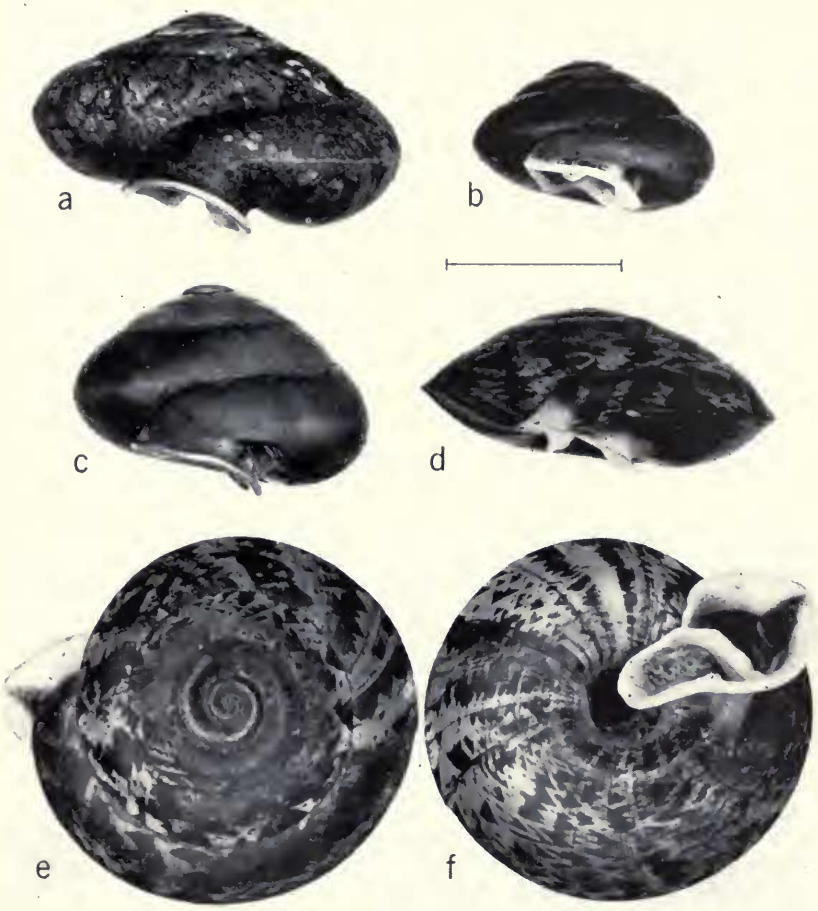


FIG. 11. Shells of: *a*, *Labyrinthus triplicatus*, Navarro, Costa Rica, CNHM 63776; *b*, *Labyrinthus q. quadridentatus*, Coto, Costa Rica, USNM 532569; *c*, *Labyrinthus q. biolleyi*, Guaitil de Pirris, Costa Rica, CM 62.5755. Holotype; *d–f*, *Labyrinthus magdalenensis*, Tierra Nueva, Magdalena, Colombia, USNM 533878. Holotype (*d*, side; *e*, top; *f*, base). Scale line equals 10 mm.

Material.—Costa Rica (ANSP 33164, CNHM 250, CNHM 127741, Edinburgh, MCZ 45116): LIMON—Cahuita (ANSP 140308); hills of Urén to 3,000 feet (Brit. Mus.). CARTAGO—Turrialba (Jackson 7105); Navarro (ANSP 226909, CNHM 63776); Platanillo at 600 meters elevation (USNM 532612); Cervantes at 1,480 meters elevation (USNM 532590); Valle de Tuis at 620 meters elevation (USNM 190276); Tuis at 650 meters elevation (CM 62.5754, MCZ 211181); Talamanca Valley (ANSP 140315).

Diagnosis.—The high, slightly sinuated parietal lamella is a little removed from the low, straight parietal lip; basal lip with one prominent tooth; lower palatal lip with one high, slightly sinuated, spade-shaped, thin lamella; periphery obtusely angulated; spire moderately to markedly elevated; sides flat or rounded; umbilicus partly covered by extension of basal and parietal lips; color brown, usually with lighter periphery; diameter 22.3–28.7 mm., H/D ratio 0.496–0.674.

Remarks.—The Venezuelan *L. leucodon* (Pfeiffer) and the Colombian *L. isodon* (Pfeiffer) are similar in general appearance, but can be easily separated. *L. leucodon* has the parietal lip concave with the tooth meeting the lip, a lower and broader lower palatal tooth, often an upper palatal tooth and the periphery acutely angulated. *L. isodon* has two basal and two palatal teeth, the parietal tooth merges with the high lower parietal lip and the upper parietal lip is greatly reduced in size. The smaller *L. quadridentatus* (Broderip) from the Pacific drainage of Costa Rica is most readily differentiated by its two basal teeth, narrower umbilicus and distinctly smaller size.

Form *aesopus* is a more elevated shell with flatter sided spire. Examples seem to be present in most sets of more than a few specimens and *aesopus* should be considered an individual variant.

The few recorded localities are all from the Atlantic drainage in the coastal lowlands or from the Atlantic slopes of the Cordillera Central and Cordillera de Talamanca. *L. triplicatus* will probably be found in Bocas del Toro, Panama and possibly may reach southern Nicaragua.

Moderate size variation is found, but only two sets of five specimens each had exact locality data. The shells from coastal Cahuita were much larger and more elevated than those from 650 meters elevation (see Table IV). The difference may be exaggerated since the material from Tuis is only a selected part of Biolley's collection. Most of his material was sold in sets of one or two individuals. Quite possibly an altitudinal cline in respect to diameter, height and H/D ratio does exist, but present evidence is inadequate.

Labyrinthus quadridentatus (Broderip, 1832)

Very few specimens are known of this species, but they immediately fall into two well characterized subspecies:

L. quadridentatus quadridentatus (Broderip, 1832) –from Golfo Dulce, Costa Rica and Comarca de Baru, Panama is smaller (diameter 15.8–18.7 mm., mean 16.7 mm.), more sharply carinated and has the basal teeth small in size.

L. quadridentatus biolleyi new subspecies—from San José and Cartago, Costa Rica is larger (diameter 19.7–21.4 mm., mean 20.4 mm.), obtusely angulated at the periphery rather than carinated, and has very prominent basal teeth.

They differ from other members of the *L. isodon* complex in having a simple parietal lamella, two basal teeth and only one palatal tooth. In appearance it is most similar to the larger *L. triplicatus* from Atlantic parts of Costa Rica and *L. sieversi* from Colombia. The latter has a closed umbilicus and a bifurcate palatal tooth, while the former has one basal tooth and is distinctly larger.

Labyrinthus quadridentatus quadridentatus (Broderip, 1832). Figures 10b, 11b.

Carocolla quadridentata Broderip, 1832, Proc. Zool. Soc. London, **1832**, p. 30—"woods near Gulf of Dulce" (=Golfo Dulce, Costa Rica).

Helix quadridentata (Broderip), Pfeiffer, 1848, Monog. helic. viv., **1**, p. 399; Reeve, 1852, Conch. Icon., *Helix*, pl. 101, fig. 557; Pfeiffer, 1853, Syst. Conch. Cab., I (12), **2**, pp. 271–272, pl. 123, figs. 9–11; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 463.

Helix (*Labyrinthus*) *quadridentatus* (Broderip), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 168–169, pl. 41, figs. 12–13.

Labyrinthus quadridentatus (Broderip), von Martens, 1892, Biol. Centr. Amer., Moll., pp. 176–177—Térraba, Costa Rica at 200–300 meters elevation (Pittier!); von Martens, 1901, Biol. Centr. Amer., Moll., pp. 628–629—Alto de Mono Tigre, near Térraba at 690–700 meters elevation in woods; El Pozo, Rio Grande de Térraba; El Pital, Valley of Rio Naranjo at 200 meters elevation; Quebrada Chenarria, Golfito and banks of Rio Coto; all in Puntarenas, Costa Rica (Pittier!).

Pleurodonte (*Labyrinthus*) *quadridentatus* (Broderip), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95.

Range.—Puntarenas, Costa Rica from the sea coast to at least 300 meters elevation and Comarca de Baru, Panama. Possibly it will be found in Chiriquí Province, Panama.

Material.—Panama: COMARCA DE BARU—Puerto Armuelles (ANSP 161830); beach near Puerto Armuelles (ANSP 226916); *Costa Rica:* PUNTARENAS—Coto at 10–20 meters elevation (USNM 471784, USNM 532569); Quebrada de la Palma, basin of Rio Coto (USNM 190284).

Diagnosis.—The high, slightly sinuated parietal lamella is distinctly removed from the parietal lip; basal lip with two teeth, inner a low broad knob, outer a high, narrow lamella; lower palatal wall with a small, high, triangular lamella; periphery acutely carinated;

umbilicus partly closed by extension of basal and parietal lips; spire strongly elevated, sides slightly rounded; color dark yellow-brown with lighter periphery. Diameter 15.8–18.7 mm. (mean 16.7 mm.), H/D ratio 0.560–0.653 (mean 0.599).

Remarks.—The differences from subspecies *biolleyi* are given below in the diagnosis of the new subspecies.

Labyrinthus quadridentatus biolleyi new subspecies. Figures 10c, 11c.

Labyrinthus quadridentatus Biolley, 1897 (not Broderip, 1832), Moluscos terr. fluv. meseta central Costa Rica, p. 11—Guatil de Pirris, Costa Rica at 800(?) meters (Biolley!).

Diagnosis.—A subspecies of *L. quadridentatus* from the Central Mountains of Costa Rica, characterized by its larger size (diameter 19.7–21.4 mm.), obtusely angulated (not acutely carinated) periphery, and stronger development of the basal lip teeth. The nominate subspecies is smaller (diameter 15.8–18.7 mm.), has an acutely carinated periphery, weaker lip teeth and is from Puntarenas and Comarca de Baru, Panama.

Holotype.—Carnegie Museum, Pittsburgh, number 62.5755. Guaitil de Pirris, Costa Rica. Collected by P. Biolley.

Description.—Shell rather small, depressed globose, obtusely angulated at periphery, with 5½ rather tightly coiled whorls. Apex and spire markedly and evenly elevated, body whorl sharply deflected at aperture, h/d ratio 0.625. Color light yellow-brown. Whorls slightly rounded, suture not deeply impressed. Surface of shell with weak radial growth lines on spire, developing moderately prominent granulations on lower part of spire, becoming quite prominent on body whorl and base of shell. Aperture deflected sharply, inclined about 60° from the shell axis, somewhat constricted by teeth and lip. Parietal lip barely free of wall, thickened internally, very slightly sinuated, and entering umbilicus at columellar margin. Parietal wall with single, prominent, simple lamella free of parietal lip. Basal lip strongly thickened internally, reflected, with posterior indentions opposite teeth, not sinuated. Basal teeth two, inner a broad, rounded knob separated from the high lamellar outer basal tooth by a sinus that is wider than the inner tooth. Palatal lip rounded, slightly compressed above, with a single high twisted lamella mounted on a triangular base. Umbilicus narrow, about half covered by extension of basal and parietal lips. Diameter 19.7 mm., height 12.3 mm.

Range.—Central mountains of Costa Rica.

Paratypes.—*Costa Rica* (MCZ 211236): SAN JOSE—Guaitil de Pirris (CM 62.5755). CARTAGO—Azahar de Cartago (ANSP 45553, Edinburgh). ALAJUELA–SAN JOSÉ border—Piedras Negras (USNM 162838).

Remarks.—The new subspecies is named in honor of its collector, the late Paul Biolley of San José, Costa Rica, who was a famous student of Costa Rican mollusks.

Size and shape variation in the few known specimens is summarized in Table IV. All known localities are from the Pacific slopes of Costa Rica and western Panama. The shell of *L. quadridentatus* is easily derivable from that of *L. triplicatus* by dwarfing, development of a second basal tooth, and more complete closing of the umbilicus. Further collecting is needed to establish the upper altitudinal ranges of both species and to see if actual intergrades occur between the nominate race of *quadridentatus* and subspecies *biolleyi*.

Labyrinthus tamsianus (Dunker, 1847). Figures 12a, 13a.

Helix tamsiana Dunker, 1847, Zeits. f. Malak., **1847**, p. 80—Puerto Cabello, Venezuela (Tams!); Pfeiffer, 1848, Monog. helic. viv., **1**, p. 399; Reeve, 1852, Conch. Icon., *Helix*, pl. 100, fig. 556; Pfeiffer, 1854, Syst. Conch. Cab., I (12), **3**, p. 466, pl. 156, figs. 28–29; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 463.

Helix (*Labyrinthus*) *tamsiana* (Dunker), Martens, 1873, Ges. Naturf. Fr., Berlin, Festschr., **1873**, p. 169—Chino, Yaracuy, Venezuela; Pilsbry, 1889, Man. Conch. (2), **5**, pp. 169–170, pl. 41, figs. 5–8.

Labyrinthus tamsianus (Pfeiffer), Jousseaume, 1889, Mem. Soc. Zool. France, **2**, p. 248—San Esteban, Venezuela.

Pleurodonte (*Labyrinthus*) *tamsiana* (Dunker), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95; H. B. Baker, 1926, Occ. Pap. Univ. Michigan Mus. Zool., **167**, pp. 20–21, pl. 13, figs. 68–70, pl. 14, fig. 74—San Esteban, La Quiguas and Bejuma, Carabobo (H. B. Baker!); Wurtz, 1955, Proc. Acad. Nat. Sci., Philadelphia, **108**, pp. 116–118, pl. 5, fig. 30.

Range.—Venezuela: Yaracuy and Carabobo.

Material.—*Venezuela* (CNHM 100135, CNHM 100210): CARABOBO—San Estaban (ANSP 175364, ANSP 140920, CNHM 117646); Bejuma (ANSP 140919); 6 miles west of Puerto Cabello (USNM 252580); Puerto Cabello (USNM 217642, USNM 336134, ANSP 4274, MCZ 74567).

Diagnosis.—The very small parietal lamella is usually short and distinctly removed from the parietal lip; basal lip with single moderately prominent knob; lower palatal wall with short, simple rather

TABLE IV.—Size and shape variation in *Labyrinthus triplicatus, L. q. quadridentatus, L. q. biolleyi, L. tamsianus, L. l. leucodon* and *L. magdalenensis*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
L. triplicatus													
CM 62.5754; Tuis, Costa Rica	5	12.7	11.8–13.7	0.35	24.2	23.5–25.9	0.44	0.525	0.500–0.556	0.010			
ANSP 140308; Cahuita, Costa Rica	5	16.3	14.7–17.2	0.46	27.7	26.5–29.3	0.46	0.590	0.533–0.646	0.018			
L. q. quadridentatus													
All	6	10.0	8.9–11.7	0.42	16.7	15.8–18.7	0.46	0.599	0.560–0.653	0.016			
L. q. biolleyi													
All	4	12.5	11.9–13.2	0.27	20.2	19.7–20.7	0.28	0.617	0.602–0.638	0.009			
L. tamsianus													
ANSP 33167; San Esteban, near Puerto Cabello, Venezuela	11	8.9	8.2–9.4	0.10	15.8	14.9–16.8	0.18	0.561	0.536–0.597	0.007			
L. l. leucodon													
ANSP 33172; La Guaira, Venezuela	10	10.5	9.9–12.0	0.20	21.9	20.6–23.5	0.28	0.477	0.430–0.547	0.011	9.2	7.9–11.4	0.40
L. magdalenensis													
USNM 533878; Tierra Nueva, Magdalena, Colombia	5	10.1	9.5–11.0	0.27	24.9	24.0–26.1	0.38	0.399	0.381–0.417	0.006			

high lamella; upper palatal wall with occasional weak tooth-like swelling on lip; periphery acutely carinated; spire markedly elevated, sides flat; color light yellowish brown. Surface very granulose, often with periostracal hairs. Diameter 12.5–17.2 mm., H/D ratio 0.536–0.642.

Remarks.—The very small, simple teeth, high, flat-sided spire and acutely carinated periphery are diagnostic. Quite possibly this is a lowland derivative of *L. leucodon*. H. B. Baker (1926, p. 20) presented data on size variation in lots he collected. His set from San Esteban had smaller shells than those taken by Swift at the same locality during the last century (see Table IV). No other material with good locality data was seen.

Labyrinthus leucodon (Pfeiffer, 1847)

Very little accurately localized material of this rather variable species was available. Eventually, several local races may be recognized. At present, two subspecies are nomenclaturally established, while material possibly representing a third is illustrated, but not described.

L. leucodon leucodon (Pfeiffer, 1847)—from several states in Northern Venezuela has the periphery acutely to obtusely angulated, the aperture moderately deflected and rather broad, and the teeth small or of average size.

L. leucodon umbrus Thompson, 1957—from Rancho Grande, Aragua has the periphery obtusely carinated, the aperture strongly deflected and rather narrow, and much larger teeth.

The *leucodon* complex is most similar to the Costa Rican *L. triplicatus* (von Martens), but differs most conspicuously in having a shorter parietal tooth that runs into the parietal lip and the lip being pure white rather than tinted.

The degree of relationship to *L. tamsianus* (Dunker) needs investigation. The latter may have the same ecological and geographic relationship that *L. triplicatus* and *L. quadridentatus* of Costa Rica seem to share.

Labyrinthus leucodon leucodon (Pfeiffer, 1847). Figures 12b, d; 13b.

Helix leucodon Pfeiffer, 1847, Zeits. f. Malak., **4**, pp. 81–82—locality unknown; Pfeiffer, 1848, Monog. helic. viv., **1**, p. 399; Reeve, 1852, Conch. Icon., *Helix*, pl. 101, fig. 558; Pfeiffer, 1853, Syst. Conch. Cab., I (12), **2**, p. 271, pl. 123, figs. 12–14—Tovar, Mérida (Dyson!) (plate issued in 1852); Mar-

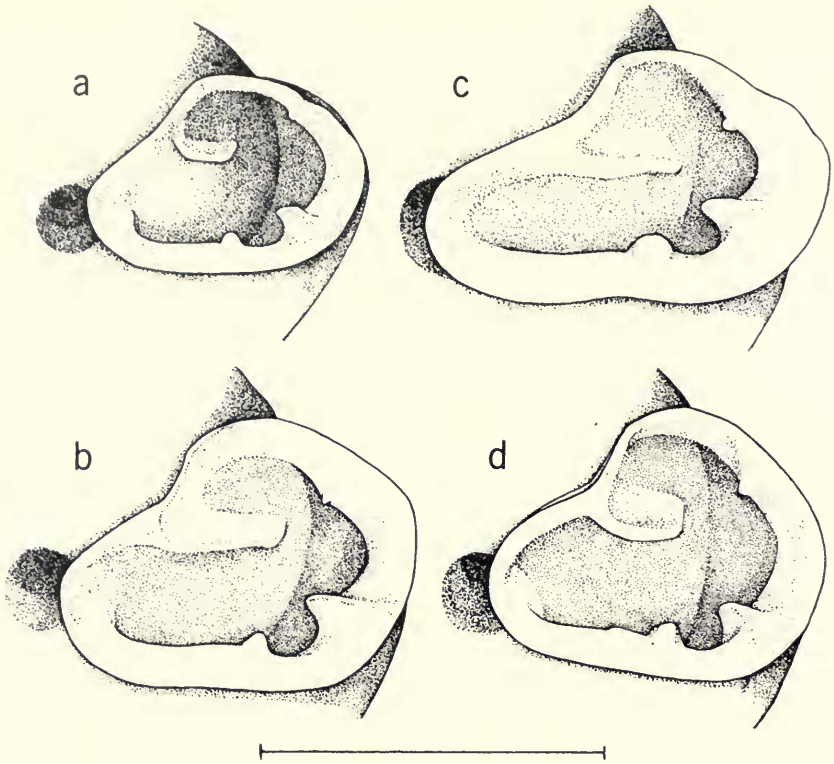


FIG. 12. Apertures of: *a*, *Labyrinthus tamsianus*, San Esteban, Venezuela, CNHM 117646; *b*, *Labyrinthus l. leucodon*, La Guaira, Venezuela, CNHM 126946; *c*, *Labyrinthus l. umbrus*, Rancho Grande, Venezuela, CNHM 64340. Paratype; *d*, *Labyrinthus leucodon*, undescribed subspecies, Venezuela. Zurich. Scale line equals 10 mm.

tens, 1873, Ges. Naturf. Fr., Berlin, Festschr., **1873**, p. 169—Caracas, D. F.; Chino, Yaracuy; Cumbre Mts. near Porto Cabello, Carabobo; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 463.

Labyrinthus quadridentatus von Martens, 1860 (not Broderip, 1832), Die Heliceen, 2nd ed., p. 155—Caracas.

Labyrinthus leucodon (Pfeiffer), Jousseaume, 1889, Mem. Soc. Zool. France, **2**, p. 248—Tovar, Venezuela.

Helix (*Labyrinthus*) *leucodon* (Pfeiffer), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 167–168, pl. 41, figs. 9–11, 14–16.

Pleurodonte (*Labyrinthus*) *leucodon* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95; H. B. Baker, 1926, Occ. Pap. Univ. Michigan Mus. Zool., **167**, p. 20.

Range.—Venezuela: Mérida, Yaracuy, Carabobo, and possibly Districto Federal.

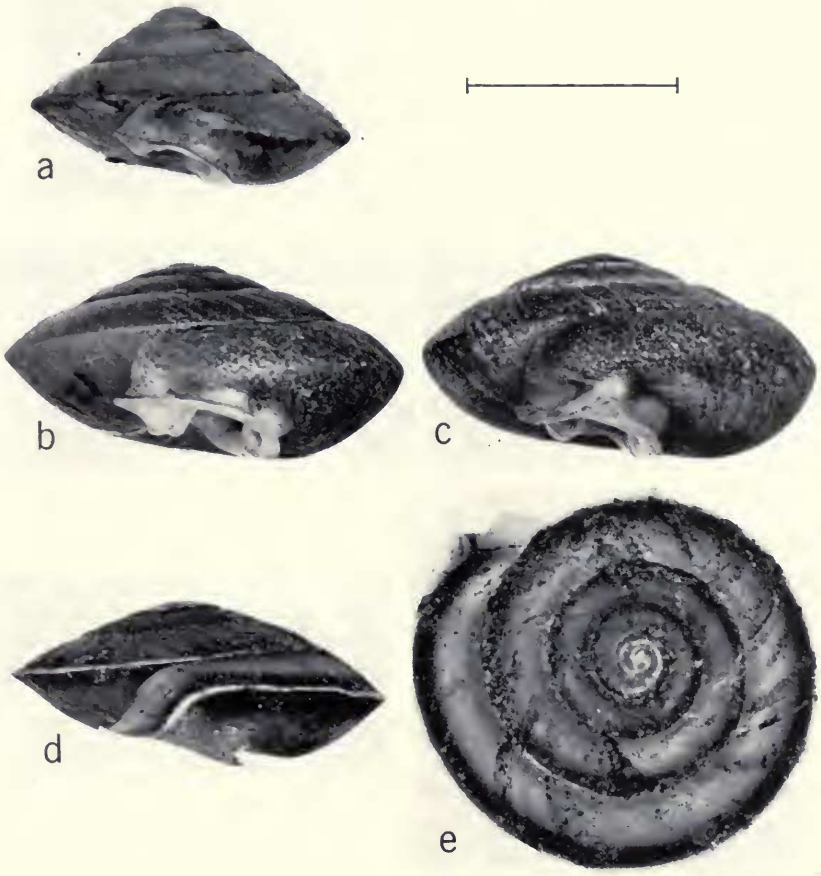


FIG. 13. Shells of: *a*, *Labyrinthus tamsianus*, San Esteban, Venezuela, CNHM 117646; *b*, *Labyrinthus l. leucodon*, La Guaira, Venezuela, CNHM 126946; *c*, *Labyrinthus l. umbrus*, Rancho Grande, Venezuela, CNHM 64340. Paratype; *d–e*, *Labyrinthus dunkeri*, Guamilito, 1,500–2,000 feet elevation, Colombia, CNHM 117649 (*d*, side; *e*, top). Scale line equals 10 mm.

Material.—*Venezuela* (CNHM 100123, Edinburgh, Zurich, USNM 316242, USNM 316046, USNM 316244, USNM 57287, ANSP 33160, ANSP 33166, ANSP 1457); Puerto Cabello (ANSP 4273); La Guiara (ANSP 33172, CNHM 126946); El Junquito, Caracas (USNM 592898); Mérida (SMF). *"Colombia"* (Zurich ex von Martens in 1854).

Diagnosis.—The high, simple parietal lamella starts descending before it runs into the parietal lip; basal lip with a broad, prominent

knob; lower palatal tooth a prominent, crescentic lamella with strong lateral buttresses; upper palatal lip often with a small tuberculate denticle; aperture moderately deflected; periphery acutely angulated; spire normally elevated, sides flat to slightly rounded; color brownish, occasionally speckled with greenish yellow. Diameter 18.9–23.5 mm., H/D ratio 0.395–0.590.

Remarks.—In about one-sixth of the individuals examined the upper palatal tooth is absent or greatly reduced. Usually it is a small conical denticle, quite like those found in many *Isomeria.* Martens (1873, p. 169) noted size, shape and tooth variations in specimens from Caracas and Puerto Cabello.

The differences between the subspecies in aperture deflection and width are obviously correlated, the greater deflection of the aperture having resulted in narrowing the aperture. Variation in tooth size probably is independently controlled.

The single shell from Caracas and the two specimens from "Colombia" differ as much from *leucodon leucodon* as does *leucodon umbrus.* The smaller teeth, much less deflected aperture with wider mouth and obtusely carinated periphery would warrant equivalent nomenclatural status, but in the absence of adequate collections recognition as a subspecies is withheld. These "subspecies" may be ecotypes, since the total amount of variation is not large.

Labyrinthus leucodon umbrus Thompson, 1957. Figures 12c, 13c.

Labyrinthus umbrus Thompson, 1957, Occ. Pap. Univ. Michigan Mus. Zool., 591, pp. 6–7, pl. 2—Rancho Grande, Aragua, Venezuela (Heatwole!).

Range.—Known only from the type locality.

Material.—Venezuela: ARAGUA—Rancho Grande (CNHM 64340).

Diagnosis.—The parietal lamella runs into the parietal lip at full height; basal lip with one very prominent knob-like tooth; lower palatal wall with high, simple, prominent lamella; upper palatal wall with a single, low triangular tooth; aperture very strongly deflected; lip strongly expanded and somewhat thickened; periphery obtusely carinated; spire moderately elevated, slightly rounded above; color brownish with yellowish green speckling; umbilicus nearly closed by the extension of the basal-parietal lip. Diameter 20.5–22.5 mm. (mean 21.2 mm.), height 9.5–11.5 mm. (mean 10.7 mm.) (data from Thompson, 1957, p. 7).

Remarks.—*L. leucodon leucodon* is more sharply carinated, has a more open umbilicus, the teeth are smaller in size, and the shell is less solid with a less sharply deflected aperture.

Only nine specimens, all from Rancho Grande, are known. While complete intergradation with *leucodon leucodon* cannot be demonstrated with available material, the differences are so minor that I have no hesitation in reducing *umbrus* to subspecific status. Etymologically, the name "*umbrus*" is incorrect and should have been "*umber*," but this has no effect on nomenclatural matters.

Labyrinthus magdalenensis new species. Figures 10d, 11d–f.

Diagnosis.—A species of *Labyrinthus* with the color pattern of *Isomeria bourcieri* (Pfeiffer), but the shape and complicated apertural dentition of the *L. isodon–L. dunkeri* complex. The direct joining of the prominent parietal lamella with the parietal lip is like *L. isodon* and *L. manueli*, but in possessing one basal and three palatal teeth, the new species is like *L. dunkeri*. The latter has much smaller palatal teeth, a parietal tooth free of the lip, and a color pattern of reddish spiral bands on a yellowish-white background.

Holotype.—United States National Museum number 533878 from Tierra Nueva, east of Fonseca, 3,700–5,000 feet elevation, Sierra Negra, Magdalena, Colombia. Collected by M. A. Carriker, Jr.

Description.—Shell of average size, lenticular, acutely carinated, peripheral keel slightly protruding, with a little more than 4⅞ normally coiled whorls. Apex and spire moderately elevated, slightly flattened above, body whorl sharply deflected at aperture, H/D ratio 0.405. Color translucent reddish-green with irregular, often triangular, yellow-white opaque maculations. Lip white, aperture reddish-brown internally. Whorls very slightly rounded with a very faint supraperipheral groove. Surface of spire with infrequent radial growth lines and occasional granulations that become very prominent on body whorl and base of shell. Aperture sharply deflected, inclined about 55° from the shell axis, constricted by lip and teeth. Parietal lip free of wall, strongly sinuated, lower portion passing directly into a high, thin, twisted parietal lamella; upper portion curving downward, becoming perpendicular to parietal lamella. Lower part of parietal lip extending into umbilicus, parallel to portion of basal lip. Basal lip thin, sinuated, strongly reflected with a single broad ridge at junction with palatal lip. Palatal lip rounded below, rather flattened above periphery, broadly reflected. Palatal teeth three: lower high, crescent shaped, slanting diagonally backward; middle tooth

located on elevated ridge just below periphery, lower, longer, more lamellate, sinuately twisted laterally; upper a narrow, prominent ridge slanting diagonally downward, located almost at mid-point of upper palatal wall. Body whorl near aperture with strong basal and lower palatal indentations behind lip. Umbilicus small, partially narrowed by extension of basal and parietal lips. Diameter 24.2 mm., height 9.8 mm.

Range.—Known only from the type locality.

Paratypes.—USNM 533878, CNHM 117645.

Remarks.—The distinctive color pattern, prominent parietal lamella continuous with the parietal lip, and three simple palatal teeth immediately separate *L. magdalenensis* from all other *Labyrinthus*. The similarly shaped *L. dunkeri* (Pfeiffer) has been found at the same locality, but in color and tooth structure is immediately separable. The more elevated, brownish, *L. isodon* (Pfeiffer) from Ocanã, Colombia is more similar in tooth structure, but is much smaller, has two basal and two palatal teeth, is less carinated and unicolored.

Size variation in the five known examples is summarized in Table IV.

Labyrinthus dunkeri (Pfeiffer, 1852). Figures 13d–e, 14a.

Helix dunkeri Pfeiffer, 1852, in Reeve's Conch. Icon., *Helix*, pl. 101, fig. 559—Andes of Colombia; Pfeiffer, 1853, Monog. helic. viv., **3**, pp. 256–257; Pfeiffer, 1854, Proc. Zool. Soc. London, **1852**, p. 157; Pfeiffer, 1854, Syst. Conch. Cab., I (12), **3**, p. 365, pl. 138, figs. 21–23; Pfeiffer, 1876, *Ibid.*, **7**, p. 463.

Helix (*Labyrinthus*) *dunkeri* (Pfeiffer), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 174–175, pl. 41, figs. 1–4.

Pleurodonte (*Labyrinthus*) *dunkeri* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95.

Range.—Colombia, from Norte de Santander to Guajira along the Sierra Perijá, probably in Est. Zuilia, Venezuela.

Material.—Colombia: SANTANDER DEL NORTE—Guamilito at 1,500–2,000 feet elevation (USNM 517810). MAGDALENA—Tierra Nueva, east of Fonseca, Sierra Negra at 3,700–5,000 feet elevation (USNM 533877); Rio Maraca, Sierra Perijá (ANSP 180017, CNHM 117648); La Palmita, trail from Loma Corredor to Ocanã (ANSP 137825); Ocanã (Zurich); western foothills of Sierra Perijá at 200–500 meters elevation (USNM 473933, CNHM 117644); near Codazzi at 600 meters elevation (USNM 599518); 5–6 km. above Manuare (ANSP); Rio Cesar Valley (USNM 534075); Airoca, Sierra

Perijá at 4,000–6,000 feet elevation (USNM 488784, USNM 488787). GUAJIRA—hills south of Carraipia (USNM 599497). ANTIOQUIA—Frontino (Edinburgh); Sonson (?) (Zurich).

Diagnosis.—The low, slightly sinuated, parietal lamella stops distinctly short of the high parietal lip; basal lip with two well defined teeth, inner a low diagonal ridge slanting from inside across lip, outer a high crescentic lamella perpendicular to lip; lower palatal wall with two teeth—lower a high, crescentic lamella, upper a triangular, slightly hooked knob; upper palatal wall with an inconspicuous short lamella located just above periphery; aperture very strongly deflected; periphery acutely carinated; spire flat; color yellowish-white with reddish-brown spiral bands bordering sutures. Diameter 18.6–24.9 mm., H/D ratio 0.345–0.466.

Remarks.—The short, simple parietal lamella, two basal teeth, two widely separated lower palatal teeth and recessed upper palatal tooth are diagnostic. Recognition is most easily accomplished, however, by the color pattern of spiral red bands on a lighter background. *L. unciger* has the same color pattern, but is much larger with only one basal tooth and a single deeply recessed lower palatal tooth. The slanted lamellar inner basal tooth of *dunkeri* is unique, while the small upper palatal tooth is only present, otherwise, in the *L. otis* group.

Ascertaining the relationships of *L. dunkeri* is quite difficult. The lower palatal teeth are of the type found in the *raimondii* series, but more widely separated, while the upper palatal tooth is like those found in the *otis* series, and the color pattern is that of *L. unciger*. It would be tempting to suggest that *L. dunkeri* in the Sierra Perijá and *L. sieversi* in the Sierra Nevada de Santa Marta are closely related, but their only similarities are in the lower palatal teeth. Pending study of the soft parts, *L. dunkeri* is placed in the *isodon* series, although it may be related to other species.

L. dunkeri ranges from 600–6,000 feet elevation in the Sierra de Perijá. Older, unconfirmed records from Antioquia may be the result of mislabeling. As often has been recorded with land shells, there is altitudinally correlated size variation in *L. dunkeri*. Comparison of the samples from Guamilito at 1,500–2,000 feet elevation (USNM 517810) and Tierra Nueva at 3,700–5,000 feet elevation (USNM 533877) show that specimens from the higher elevation are significantly larger, but not significantly different in proportions. In respect to height ($n=10$, $t=5.815$) and diameter ($t=6.933$) the probability level is much less than 0.001, while for the differences in proportion (H/D ratio, $t=1.119$) the probability level lies between 0.2 and 0.3

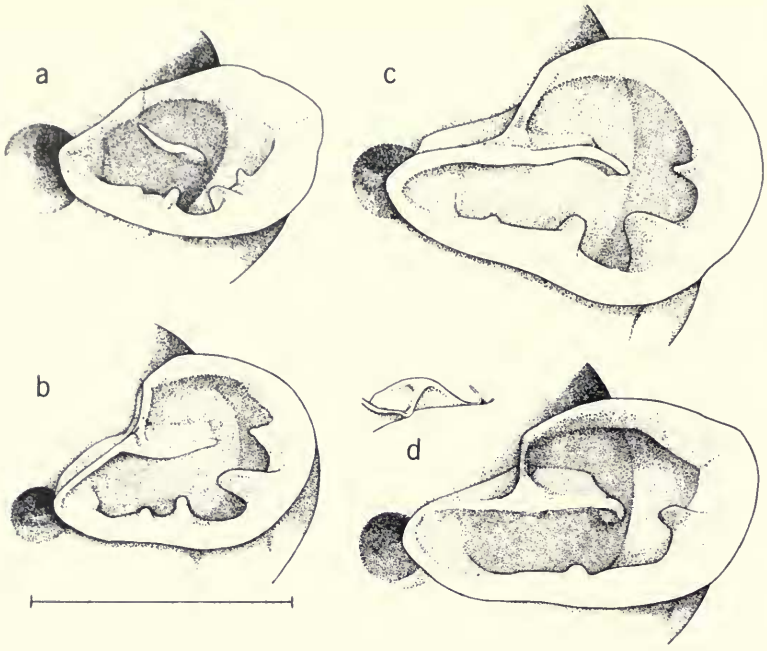


FIG. 14. Apertures of: *a*, *Labyrinthus dunkeri*, Guamilito, 1,500–2,000 feet elevation, Colombia, CNHM 117649; *b*, *Labyrinthus isodon*, Ocaña, Colombia, ANSP 104823; *c*, *Labyrinthus vexans*, Frontino, Colombia. Zurich, ex Mousson. Probably a paratype; *d*, *Labyrinthus manueli*, Mera, Ecuador, CNHM 126947. Scale line equals 10 mm.

that they could have been drawn from the same population. Such size differences and "dwarfing effects" have most frequently been shown to correlate with rainfall and moisture factors and the apparent "altitude correlation" has been subsequently demonstrated to reflect the common phenomenon of increase in rainfall with increase of elevation on montane slopes. Presumably such a moisture factor operates in size variation in *L. dunkeri*, but no ecological data are available for the reported localities.

L. magdalenensis was also collected at Tierra Nueva, but the ecological relationships or differences are unknown.

Labyrinthus isodon (Pfeiffer, 1853). Figures 14b, 15a.

Helix isodon Pfeiffer, 1853, *in* Reeve's Conch. Icon., *Helix*, pl. 149, fig. 965—Western Colombia; Pfeiffer, 1853, Monog. helic. viv., **3**, p. 257; Pfeiffer, 1854, Proc. Zool. Soc. London, **1852**, pp. 84–85; Pfeiffer, 1854, Syst. Conch. Cab., I (12), **3**, p. 490, pl. 160, figs. 19–21; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 463.

Helix (*Labyrinthus*) *isodon* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 175, pl. 64, figs. 19–21.

Pleurodonte (*Labyrinthus*) *isodon* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95.

Range.—Ocanã, Norte de Santander, Colombia is the only recorded locality.

Material.—*Colombia:* NORTE DE SANTANDER—Ocanã (ANSP 104823, CNHM 127742, Zurich, Edinburgh); ? Mt. Lucero (Zurich).

Diagnosis.—The high sinuately twisted parietal lamella attaches at full height to the lower parietal lip, but forms a distinct angle at the junction, while the upper part of the parietal lip is greatly reduced in height; basal lip with two prominent, crescentic teeth, the inner smaller; lower palatal wall with two subequal teeth, upper a small triangular lamella twisted upward, lower one a much higher cres-

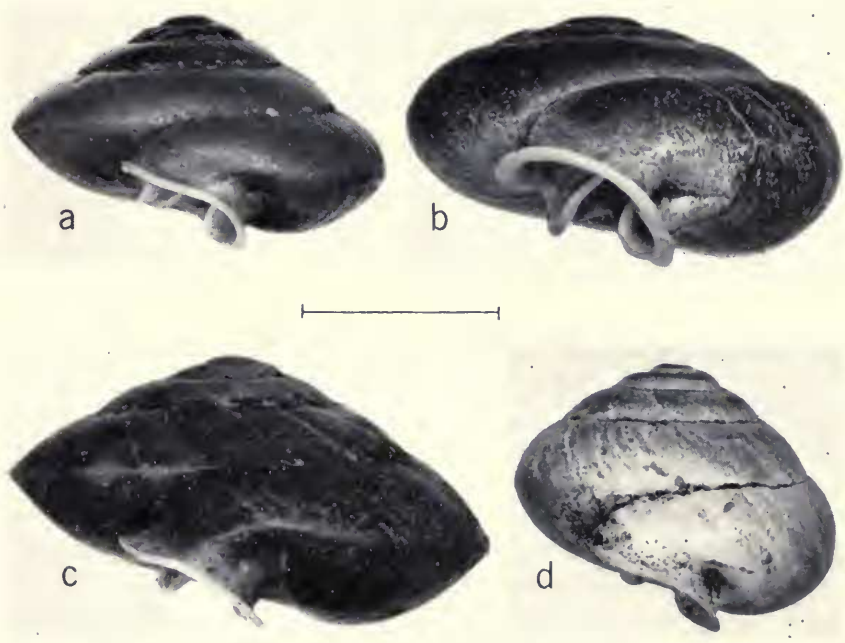


FIG. 15. Shells of: *a*, *Labyrinthus isodon*, Ocaña, Colombia, ANSP 104823; *b*, *Labyrinthus vexans*, Frontino, Colombia. Zurich, ex Mousson. Probably a paratype; *c*, *Labyrinthus manueli*, Mera, Ecuador, CNHM 126947; *d*, *Labyrinthus sieversi*, San Miguel, Sierra Nevada de Santa Marta, Colombia, ANSP 140048. Scale line equals 10 mm.

TABLE V.—Size and shape variation in *Labyrinthus dunkeri* and *L. manueli*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
L. dunkeri													
USNM 517810; Guamilito, Santander del Norte, Colombia	7	8.2	7.7–9.0	0.17	20.3	19.5–21.0	0.18	0.404	0.377–0.462	0.011			
USNM 599497; Carraipia, Goajira, Colombia	4	9.5	9.0–9.9	0.24	22.0	21.3–23.0	0.42	0.422	0.395–0.460	0.015			
ANSP 180017; Rio Maraca, Perija, Colombia	10	9.0	8.4–10.1	0.21	22.7	21.4–24.0	0.24	0.399	0.358–0.459	0.010			
USNM 533877; Tierra Nueva, Magdalena, Colombia	5	9.8	9.1–10.3	0.21	23.2	21.8–24.3	0.43	0.420	0.403–0.445	0.007			
USNM 473933; Sierra de Perija, Colombia	5	9.1	8.9–9.5	0.10	23.3	22.2–24.9	0.46	0.389	0.347–0.410	0.011			
L. manueli													
Jackson 10159; Santo Domingo de los Colorados, Ecuador	4	12.3	11.4–13.2	0.38	24.2	22.9–26.0	0.72	0.505	0.498–0.510	0.003	12.0	10.3–14.3	0.90
Jackson 7834; Mera, Ecuador	4	13.5	11.6–14.6	0.65	27.1	22.9–28.7	1.39	0.499	0.477–0.521	0.010	10.5	10.0–11.0	0.23

centic blade; aperture moderately deflected; periphery acutely to obtusely angulated; spire markedly and evenly elevated, sides flat to gently rounded; color dark yellow brown. Diameter 16.0–21.4 mm., H/D ratio 0.560–0.651.

Remarks. —The two palatal teeth and less perfect junction of the parietal lamella with the lower parietal lip easily separate this species from *L. manueli* (Higgins) from Ecuador, which seems to be the nearest relative. Only the five specimens labeled "Ocanã" had recognizable data. The single shell from the Mousson collection labeled "Mt. Lucero" was collected by Stäme and received from Landolt in 1875. The location of "Mt. Lucero" is unknown.

Labyrinthus vexans (Dohrn, 1875). Figures 14c, 15b.

Helix (*Isomeria*) *vexans* Dohrn, 1875, Nachr. d. Malak. Gesell., **7**, p. 57—Cañasgordas, Antioquia, Colombia; Dohrn, 1875, Jahr. deutsch. Malak. Gesell., **2**, pp. 294–295, pl. 10, figs. 3–4; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 591; Dohrn, 1886, Syst. Conch. Cab., I (12), **4**, p. 626, pl. 180, figs. 3–4; Pilsbry, 1889, Man. Conch. (2), **5**, pp. 158–159, pl. 42, figs. 38–39, pl. 44, figs. 5–6.

Pleurodonte (*Isomeria*) *vexans* (Dohrn), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Labyrinthus (*Ambages*) *vexans* (Dohrn), Zilch, 1960, Handb. Paläozool. (6), **2**, (4), p. 603, fig. 2117—Cañas Gordas, Colombia (lectotype).

Range.—Known only from the type collection.

Material.—"New Granada" (ANSP 63598, MCZ 79494). *Colombia:* ANTIOQUIA—Frontino (Zurich).

Diagnosis.—The parietal lamella is high and continuous with the lower portion of the parietal lip, while the upper parietal lip is greatly reduced and inserts almost perpendicularly into the lower portion; basal lip nearly straight with one very prominent crescentic lamella and a small inner knob or diagonal lamella; lower palatal lip with a high, thin lamella; upper palatal lip with a lower high lamella; umbilicus partly closed by parietal and basal lips; periphery obtusely angulated. Diameter 26.0–28.2 mm. (mean 27.1 mm.), H/D ratio 0.503–0.542 (mean 0.526).

Remarks.—The teeth are very similar to those found in *L. isodon*, except for the lack of an angle at the junction of the parietal lamella and lip. In form and shape, *vexans* is quite similar to *L. manueli*, but differs in being less carinated and having an upper palatal tooth. No recent collections of this species are known.

Labyrinthus manueli Higgins, 1872. Figures 14d, 15c.

Helix quadridentata Hidalgo, 1870 (not Broderip, 1832), Viaje al Pacifico, Moll., pp. 16–17, pl. 1, figs. 8–9—Napo, Ecuador.

Labyrinthus manueli Higgins, 1872, Proc. Zool. Soc. London, **1872**, p. 686, pl. 56, figs. 5, a—Macas, Ecuador.

Helix manoeli (*sic*) (Higgins), Pfeiffer, 1876, Monog. helic. viv., **7**, p. 462.

Labyrinthus manceli (*sic*) (Higgins), Miller, 1878, Malak. Blätt., **25**, p. 167.

Labyrinthus manueli Higgins, Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 64—Napo, Ecuador.

Labyrinthus quadridentata Hidalgo (not Broderip, 1832), Miller, 1878, Malak. Blätt., **25**, p. 167; Cousin, 1887, Bull. Soc. Zool. France, **12**, pp. 64–65.

Helix (*Labyrinthus*) *manueli* (Higgins), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 166–167, pl. 41, figs. 20–21, pl. 42, figs. 27–28, pl. 55, figs. 15–16; Reibisch, 1896, Abhl. Naturwiss. Gesell., Isis, Dresden, **1896**, p. 55—Mapoto, Pastaza Valley, Ecuador.

Pleurodonte (*Labyrinthus*) *manueli* (Higgins), Pilsbry, 1894, Man. Conch. (2), **9**, p. 96.

Range.—Upper Amazonian slopes of Ecuador with one record from the headwaters of a tributary of the Rio Guayas on the Pacific slopes.

Material.—*Ecuador* (ANSP 33165, ANSP 107809, Zurich, Edinburgh): Santo Domingo de los Colorados (Jackson 10159); Abitagua, Pastaza Valley (Jackson 5714, MCZ 90941); Puyo (Jackson 6235); Mera (Jackson 7834, CNHM 126947); Antisana (Jackson 10145); Napo (MCZ 156694); Guama Hill, 2,000 feet elevation, Baños, Tungurahua (MCZ 65725); Méndez, Upper Paute River (USNM 426536).

Diagnosis.—The single, high, curved parietal tooth is continuous with the lower parietal lip; upper parietal lip much reduced in size, inserting perpendicularly onto lamella; basal lip nearly straight, with 1–2 low knobs; inner basal knob moderately prominent, low and rounded, outer basal knob varying from absent to a low swelling or as large as inner basal tooth; lower palatal wall with single crescentic lamella, buttressed laterally; spire moderately and evenly elevated; color brownish, with or without a lighter peripheral band. Diameter 21.6–30.1 mm. (mean 25.9 mm.), H/D ratio 0.465–0.560 (mean 0.502).

Remarks.—*L. isodon* differs from *L. manueli* in having an imperfect union of the parietal lamella and lip, two palatal teeth and two strongly developed basal teeth. Other *Labyrinthus* are easily separated by differences in tooth number or in having the parietal tooth differently constructed. The presence or absence of the second basal tooth is about equally frequent. No set contained more than four specimens, so that there is no data indicating if this variation is geo-

graphically correlated. Specimens from Abitagua, Puyo and Mera are several millimeters larger than those from Santo Domingo de los Colorados, Méndez and Antisana, but the numbers involved (4, 3, 4, 4, 1, and 2, respectively) are too small for meaningful statistical analysis.

Group of *Labyrinthus raimondii*

Several species described from the Upper Amazonian basin agree in having one simple parietal tooth, a single basal knob and a markedly bifurcated lower palatal tooth. Occasionally there is a thread-like trace on the upper palatal lip that follows the line of the periphery. Sometimes this trace is represented by a lighter color zone. Authenticated records range from the Upper Caquetá drainage of Colombia south to the Madre de Dios drainage of southeastern Peru and east into Pará, Brazil. Most of the specimens come from the foothills of the mountains in Caquetá and Amazonas, Colombia; Ecuador; and Loreto, Peru; but a few are known from San Martín, Libertad, Junín, Cusco and Madre de Dios, Peru. There are two valid records from Pará, Brazil, and a few records from Amazonas. A species from the Sierra Nevada de Santa Marta, Magdalena, Colombia is also classified here.

Much of this area has high rainfall, but conditions vary from extreme seasonal patterns to almost continual downpour. Eventually the large size variation in the shells may be correlated with moisture conditions. Presently this is impossible. There is a confusing mass of minor changes in size, degree of carination, openness of umbilicus, color of the lip, size and shape of the parietal lamella and degree of deflection of the aperture. Several specific names are available, but species units cannot be recognized. The shells show insufficient characters to create other than arbitrary, artificial divisions. One or two forms seem to be moderately well characterized, but their mosaic distribution with related morphs complicates intelligent treatment of the complex. The meaning of observed variation cannot be evaluated because only a few sets contain more than three specimens, ecologic information is totally absent, there have never been two collections from the same locality at different times, and soft parts of only one form are available. In view of the extreme variability and uncertain classification, no attempt has been made to diagnose most of the forms.

Particular difficulty is experienced in separating the several relatively small species. The dividing line is especially tenuous between *L. ellipsostomus* and *L. diminutus* since individuals were seen that

could be classified as large, less sharply carinated *L. ellipsostomus*, or small, thin-shelled, rather sharply carinated *L. diminutus* or *L. pronus*. Unfortunately, most such material was from older collections and lacked accurate locality data. It is quite possible that *ellipsostomus* will be shown to be a form of the Amazonian flood-plain regions of Brazil with *diminutus* and *pronus* representing, respectively, southern and northern derivatives of only subspecific status. The rather well-marked *L. leprieurii* differs in having the sinuated parietal lamella inserting perpendicularly into the parietal lip, while in only a few isolated examples of the other species does the parietal lamella even slightly touch the parietal lip. *L. sieversi* from the Sierra Nevada de Santa Marta, Magdalena, Colombia is geographically isolated and differs in having two distinct basal teeth, rounded periphery and a closed umbilicus. It is classified with the *raimondii* series since it has the same lower palatal dentition, but stands quite isolated in other characters. *L. sieversi* could be related to *L. clappi* or else a very specialized member of the *L. isodon* complex. *L.* sp. is very similar to *L. sieversi*, but has a less completely closed umbilicus and only one basal tooth.

The larger species are more easily distinguished. *L. tarapotoensis* and its subspecies *baeri* have a white lip and obtusely angulated periphery; *L. raimondii* has a brown lip and acutely angulated periphery. *L. furcillatus* a white to brown lip with the arms of the lower palatal tooth widely separated and an obtusely angulated periphery; *L. bifurcatus* is a much higher shell with very narrow umbilicus, obtusely angulated periphery and white or brown lip.

It must be emphasized that these divisions are arbitrary and may not accurately reflect relationships. *L. leprieurii*, *L. pronus* and *L. tarapotoensis baeri* are reported from the same locality, Doma Santa Clara, 6° 55′ S, Ucayali River Valley, Loreto, Peru, based on a few dead collected shells in the USNM. Presently available specimens can be segregated into the nomenclatural units outlined below, but provision of adequate materials for study could radically alter the proposed classification. Since the taxa are so similar in appearance, use of the key will be greatly facilitated by reference to the figures.

To some extent, the species show geographic isolation (fig. 58), although there are no recorded localities for *L.* sp., *L. bifurcatus* or *L. furcillatus*. *L. sieversi* is isolated in Magdalena, Colombia, but the remaining species are found in the Amazonian basin from the Rio Tapajóz in Pará, Brazil to Caquetá, Colombia and south to Madre de Dios, Peru. Most records are from the Amazonian foothill region

TABLE VI.—Size variation in *L. raimondii* complex

Form	Diameter of type	Observed material: Diameter in mm. Mean	Diameter in mm. Range	H/D ratio Mean	H/D ratio Range	D/U ratio Mean	D/U ratio Range	Number of specimens measured
L. species	..	....	21.0–23.0	.....	0.571–0.617	....	imperforate	2
L. bifurcatus	37	....	31.4–32.4	.....	0.519–0.535	....	17.1–19.6	2
L. raimondii (dwarf form)	..	25.4	22.4–28.2	0.482	0.436–0.505	12.4	9.7–14.1	5
L. diminutus	27	25.7	21.5–30.0	0.462	0.387–0.496	9.4	6.2–17.0	32
L. pronus	28	26.1	24.4–28.5	0.423	0.358–0.459	7.5	6.6–8.1	3
L. t. tarapotoensis	34	34.0	30.8–37.5	0.444	0.426–0.471	10.1	9.1–11.2	7
L. t. baeri	47	42.0	38.9–44.0	0.424	0.359–0.473	11.4	9.6–13.9	11
L. raimondii	45	40.4	31.5–48.6	0.426	0.358–0.508	8.4	6.1–11.9	113
L. furcillatus	44	43.3	35.4–46.9	0.441	0.403–0.461	10.6	6.8–15.7	11

of the Andes. *L. ellipsostomus* from the Rio Solimoes and Santa Fe de Bogotá may range from Amazonas, Brazil into the upper Orinoco drainage of Colombia, but the enigmatic "Santa Fe de Bogotá" gives no information as to the northern limit of its range. *L. pronus* from Loreto and San Martín (Ucayali and Huallaga drainages) and *L. diminutus* from Cusco, Madre de Dios and Junín in Peru, plus the Juruá River in Amazonas, Brazil could be (as mentioned above) derivatives of *L. ellipsostomus*. *L. leprieurii* from Loreto and San Martín, Peru has been collected with *L. pronus* and may also have been derived from *L. ellipsostomus*. The larger white-lipped *L. tarapotoensis* ranges from 975–5,000 feet in scattered areas of northern and eastern Peru, while the larger subspecies *baeri* has been reported only from San Martín and Loreto. The widest ranging species is *L. raimondii*, recorded from Caquetá, Colombia south to southern Loreto, Peru and east to the confluence of the Rio Tapajóz and Amazon in Pará, Brazil. Particularly puzzling in the latter species is the appearance of a dwarf variety (see Table VI) with narrower umbilicus, higher spire and much smaller size, but otherwise very similar to *raimondii*. This peculiar form may represent an unnamed species, but in view of the variability and uncertain classification, nomenclatural recognition has been withheld.

KEY TO THE *LABYRINTHUS RAIMONDII* COMPLEX

1. Umbilicus completely closed.....2
   Umbilicus at least slightly open.....3
2. Basal lip with two teeth; Magdalena, Colombia.
   Labyrinthus sieversi (von Martens, 1889)
   Basal lip with one tooth; probably Ecuador or Peru.....*Labyrinthus* sp.
3. Parietal lamella free of parietal lip or just reaching lip.....4
   Parietal lamella merging perpendicularly with parietal lip at full height (fig. 16b)
   Labyrinthus leprieurii (Petit, 1840)
4. Periphery obtusely angulated or rounded.....5
   Periphery acutely angulated, often with protruding keel.....8
5. Umbilicus moderately open, H/D ratio less than 0.500.....6
   Umbilicus slightly open, H/D ratio more than 0.500
   Labyrinthus bifurcatus (Deshayes, 1838)
6. Arms of lower palatal tooth close together (fig. 21a), lips white.....7
   Arms of lower palatal tooth set far apart (fig. 21e), lips white or brown.
   Labyrinthus furcillatus (Hupé, 1853)
7. Diameter 38–44 mm., parietal lamella often meeting lip.
   Labyrinthus tarapotoensis baeri Dautzenberg, 1902
   Diameter 30–38 mm., parietal lamella not meeting lip.
   Labyrinthus t. tarapotoensis (Moricand, 1858)
8. Diameter usually much less than 30 mm.....9
   Diameter usually much more than 31 mm.
   Labyrinthus raimondii (Philippi, 1867)

9. Lip white.....10
   Lip brown.....*Labyrinthus raimondii* (Philippi, 1867) dwarf form
10. Periphery acutely angulated, but not keeled, shell thick.....11
    Periphery with knife-edge keel; shell thin.
    Labyrinthus ellipsostomus (Pfeiffer, 1854)
11. Spire flat or only slightly elevated; Loreto and San Martín, Peru.
    Labyrinthus pronus Pilsbry, 1932
    Spire normally elevated; Junín, Cusco and Madre de Dios, Peru; Amazonas, Brazil.....*Labyrinthus diminutus* Gude, 1903

Labyrinthus sieversi (von Martens, 1889). Figures 15d, 16a.

Helix sieversi von Martens, 1889, Conch. Mitteil., **3**, pp. 7–8, pl. 41, figs. 5–6—below Oblo at 100–300 meters elevation, Sierra Nevada de Santa Marta, Magdalena, Colombia (Sievers!).

Caracolus (*Labyrinthus*) *sieversi* (von Martens), Pilsbry, 1892, Man. Conch. (2), **8**, pp. 263–264.

Pleurodonte (*Labyrinthus*) *sieversi* (von Martens), Pilsbry, 1894, *op. cit.* (2), **9**, p. 95, pl. 22, figs. 7–8.

Range.—Colombia: Sierra Nevada de Santa Marta, Magdalena, from at least 300–5,500 feet elevation.

Material.—Colombia: MAGDALENA—Los Gorros, old trail from Fonseca to Ríohacha, northeast spur of Sierra Nevada de Santa Marta at 2,500 feet elevation (USNM 488812); San Miguel, Sierra Nevada de Santa Marta at 5,500 feet elevation (ANSP 140048).

Diagnosis.—The high, slightly sinuated parietal lamella does not reach the edge of the thick parietal callus; parietal lip appressed to wall; umbilicus closed by basal lip and parietal callus; basal lip with two prominent teeth; two lower palatal teeth, upper a triangular somewhat hooklike knob slanting upward, lower a high diagonally slanted lamella; aperture strongly deflected; periphery rounded, very faint trace of angulation; spire high, slightly rounded; color brownish. Diameter 17.4–19.0 mm., H/D ratio 0.650–0.702.

Remarks.—The completely closed umbilicus, two basal teeth, and parietal lip appressed to the penultimate whorl immediately separate *L. sieversi* from other members of the *L. raimondii* complex. It somewhat resembles *L. clappi* Pilsbry, but the form of the teeth is much nearer to that found in *L. ellipsostomus* and *L. leprieurii*. Only three specimens were seen during this study.

Labyrinthus species. Figure 19a–c.

Helix bifurcata var. Pfeiffer, 1852, Syst. Conch. Cab., I (12), **2**, p. 207, pl. 105, figs. 2–4; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 305; Pilsbry, 1889, Man. Conch. (2), **5**, pp. 170–171, pl. 42, figs. 29–31, pl. 64, figs. 24–25.

Range.—Unknown.

Material.—Peru: SAN MARTIN—Moyobamba (Edinburgh, CNHM 132548).

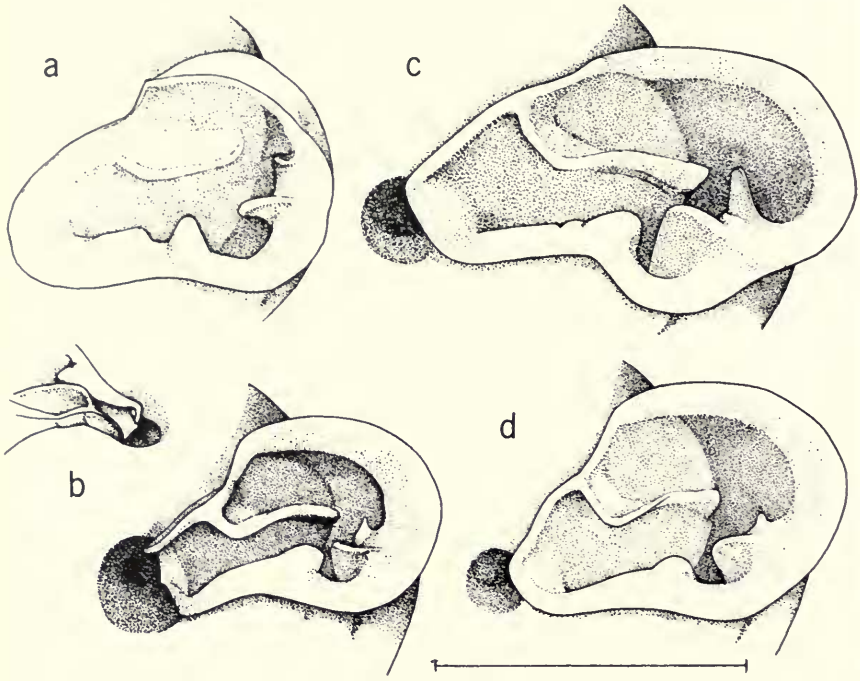


FIG. 16. Apertures of: *a, Labyrinthus sieversi*, San Miguel, Sierra Nevada de Santa Marta, Colombia, ANSP 140048; *b, Labyrinthus leprieurii*, "French Guiana," CNHM 40763; *c, Labyrinthus leprieurii*, "Guyana." Zurich, ex Petit. Paratype; *d, Labyrinthus leprieurii*, form *auriculina*, Meobamba, Peru, CNHM 40775. Scale line equals 10 mm.

Remarks.—In this species the umbilicus has become completely closed and the spire is markedly elevated and rounded above. First recognized and figured by Pfeiffer (1852), the only locality record is that cited above. While it may be correct, I suspect that it was added to the specimens based on the recorded locality for *L. bifurcatus* in Pfeiffer's *Monog. helic. viv.* Although unquestionably distinct from all described species, nomenclatural recognition should be withheld until adequately localized material is available. *L. sieversi* from Magdalena, Colombia immediately differs in having two basal teeth, but is otherwise similar.

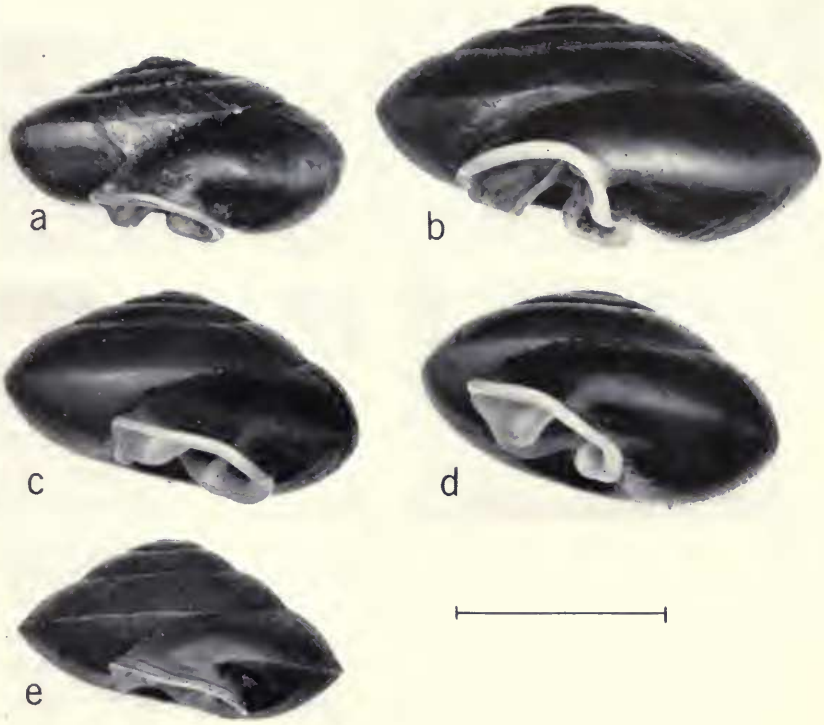


FIG. 17. Shells of: *a*, *Labyrinthus leprieurii*, "French Guiana," CNHM 40763; *b*, *Labyrinthus leprieurii*, "Guyana." Zurich, ex Petit. Paratype; *c*, *Labyrinthus leprieurii*, form *auriculina*, Meobamba, Peru, CNHM 40775; *d*, *Labyrinthus leprieurii*, form *auriculina*, "Guyana." Zurich; *e*, *Labyrinthus ellipsostomus*, Bogotá, Colombia, ANSP 109259. Scale line equals 10 mm.

Labyrinthus ellipsostomus (Pfeiffer, 1854). Figures 17e, 18.

Helix ellipsostoma Pfeiffer, 1854, *in* Reeve's Conch. Icon., *Helix*, pl. 198, fig. 1389—Santa Fe de Bogotá, Colombia; Pfeiffer, 1855, Proc. Zool. Soc. London, **1854**, p. 288; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 307; Pfeiffer, 1876, *Ibid.*, **7**, p. 463.

Helix yatesii Pfeiffer, 1855, Proc. Zool. Soc. London, **1855**, pp. 92–93, pl. 31, figs. 13–14—Solimoes River, Brazil; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 306; Pfeiffer, 1876, *Ibid.*, **7**, p. 462.

Helix (*Pleurodonte*) *yatesii* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 173, pl. 42, figs. 34–37.

Helix (*Pleurodonte*) *ellipsostoma* Pfeiffer, Pilsbry, 1889, *Ibid.* (2), **5**, pp. 173–174, pl. 41, fig. 22.

Pleurodonte (*Labyrinthus*) *yatesi* (Pfeiffer), Pilsbry, 1894, *Ibid.* (2), **9**, p. 95; von Ihering, 1905, Rev. Museu Paulista, **6**, pp. 456–457—Regiao de San

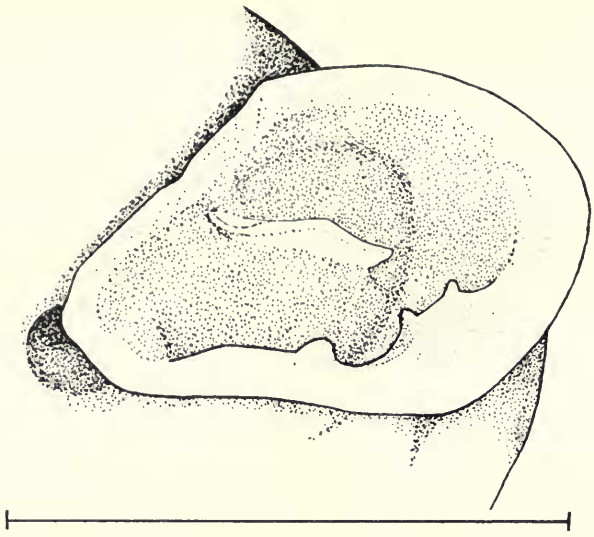


FIG. 18. Aperture of: *Labyrinthus ellipsostomus*, Bogotá, Colombia, ANSP 109259. Scale line equals 10 mm.

Felipe, Rio Juruá, Est. Amazonas, Brazil (Garbe!); Lange de Morretes, 1949, Arq. Museu Paranaense, 7, p. 163.

Pleurodonte (*Labyrinthus*) *ellipsostoma* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), 9, p. 95.

Range.—Probably upper Orinoco drainage of Colombia and the upper Amazonian basin of Brazil and Peru.

Material.—Brazil (USNM 307448, ANSP 1458, ANSP 33171, ZMA); AMAZONAS—Rio Solimoes (Edinburgh, CNHM 127744, ex Hugh Cuming, probably paratypes); Rio Juruá (Brit. Mus. 1903.4. 14.4). *Peru:* SAN MARTIN—Moyobamba (ANSP 33159, SMF 26379); LORETO—Ucayali (MCZ 74570); ?banks of the Rio Marañón (Marignanufer in Zurich collection). *Colombia* (ZMA): CUNDINAMARCA—(Santa Fe de) Bogotá (ANSP 109259, Edinburgh, CNHM 127743).

Diagnosis.—The high, thin, sinuately twisted parietal lamella stops short of the raised parietal lip; basal lip with a prominent, crescentic lamellar ridge; lower palatal lip only moderately indented with two teeth joined by an elevated ridge; lower tooth a thin crescentic, blade-like lamella pointed perpendicularly toward parietal wall; upper lower palatal tooth a narrow, curved hook-like structure pointing toward upper palatal margin; aperture strongly deflected; umbilicus narrow to moderately open; periphery acutely angulated or

keeled; spire moderately elevated, sides flat to slightly rounded; color yellow brown. Diameter 17.3–24.0 mm., H/D ratio 0.432–0.541.

Remarks.—The original descriptions indicated that *yatesi* (diameter 24 mm.) was distinctly larger than *ellipsostomus* (diameter 20 mm.). Material seen during this study was exactly opposite, the *ellipsostomus* (see Table VII) being larger than the probable paratypes of *yatesi*. The tooth structure of the two sets is identical and no hesitation is felt in uniting the species. Unfortunately, all known material dates from collections in the last century and, except for the record by von Ihering (1905), no exact locality is known.

The nearest relatives are apparently *L. leprieurii* (Petit) from French Guiana(?) and Peru, in which the parietal lamella is joined to the parietal lip and the periphery is much less acutely angulated; and the thicker shelled, less acutely keeled *L. diminutus* and *L. pronus*. Both *L. dunkeri* (Pfeiffer) and *L. isodon* (Pfeiffer) have similar shape and form, but are easily distinguished by having two basal teeth.

Size range was moderate (diameter 17.3–24.0 mm., mean 19.4 mm.) and the degree of elevation average (H/D ratio 0.432–0.541, mean 0.481). The umbilicus varied from very narrow to slightly open (D/U ratio 10.3–24.5, mean 16).

Labyrinthus diminutus Gude, 1903. Figures 19d–f, 21a.

Labyrinthus baeri Dautz. var. *diminuta* Gude, 1903, Proc. Malac. Soc. London, **5** (4), p. 262, pl. 7, figs. 1–4—Perené, Dept. Junín at 900 meters elevation and Sagarmo at 1,000 meters elevation, Peru (Rosenberg!).

Pleurodonte (*Labyrinthus*) *Da Costiana* Preston, 1907, Ann. Mag. Nat. Hist. (7), **20**, pp. 490–491, fig. 3—Chanchamayo, Junín, Peru.

Pleurodonte (*Labyrinthus*) *dacostiana* Preston, Haas, 1952, Fieldiana: Zool., **34** (9), p. 117—Hacienda Cadena, Dist. Marcapata, Prov. Quispicanchi, Dept. Cusco, Peru at 1,000 meters elevation (Kalinowski!).

Range.—Peru, Junín in the Apurímac drainage; Cusco and Madre de Dios in the drainage of the Madre de Dios; Rio Juruá in Brazil.

Material.—*Peru* (Edinburgh): JUNÍN —Perené at 900 meters (Edinburgh, types of *diminuta* Gude); Sagarmo(?) at 1,000 meters elevation (CNHM 40770, paratype of *diminuta* Gude, 1903); Chanchamayo (USNM 202504, holotype of *dacostiana* Preston, ANSP 45551, paratype, ANSP 45552); Chanchamayo Valley at 1,100 meters (USNM 601829); Chanchamayo Valley at 1,300 meters (SMF 141093). CUSCO—Hacienda Cadena, Dist. Marcapata, Prov. Quispicanchi (CNHM 28152); Rio Paucartambo, Rio Perené (CNHM 107821).

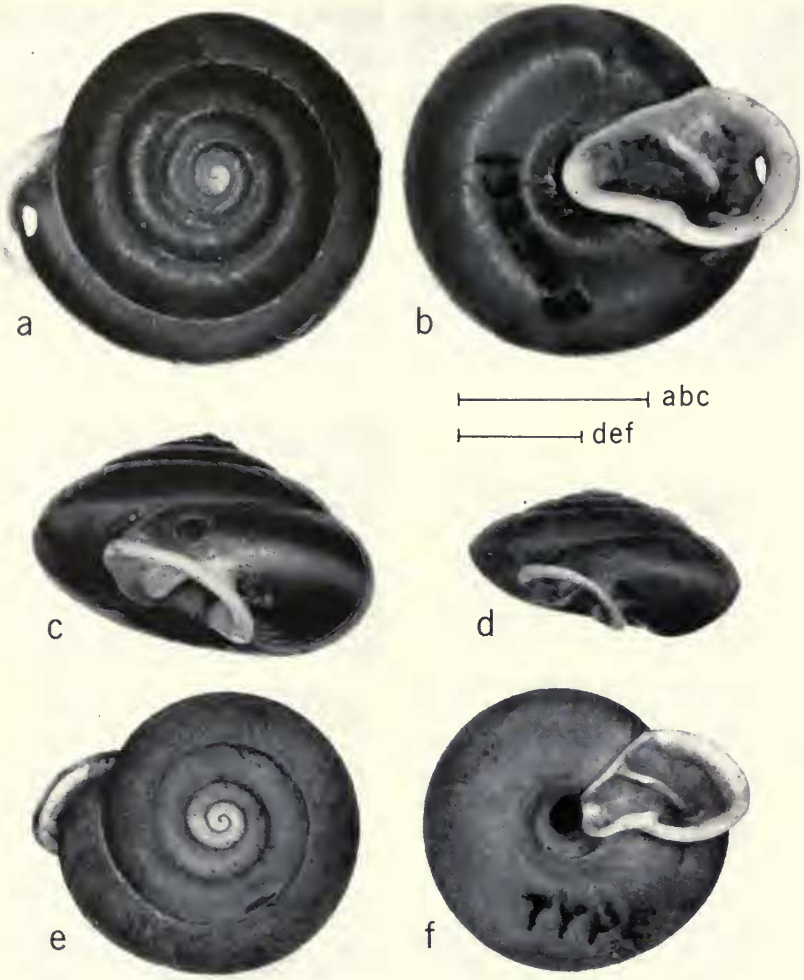


FIG. 19. Shells of: *a–c*, *Labyrinthus* sp., Meobamba, San Martín, Peru, CNHM 132548 (*a*, top; *b*, base; *c*, side); *d–f*, *Labyrinthus diminutus*, Perené, Junín, Peru. Edinburgh. Lectotype (*d*, side; *e*, top; *f*, base). Scale lines equal 10 mm.

MADRE DE DIOS—Boca Inambari, near Manu (CNHM 53634). *Brazil:* AMAZONAS—Rio Juruá (USNM 171453).

Remarks.—The specimens from the Madre de Dios drainage are flatter, slightly more sharply angulated and more widely umbilicated than the types of *diminutus*, but agree perfectly in the apertural dentition. There seems to be very little difference between *diminutus* and *pronus* from Libertad and Loreto. The latter is flatter above, with

TABLE VII.—Size and shape variation in *Labyrinthus ellipsostomus*, *L. diminutus*, *L. tarapotoensis baeri* and *L. furcillatus*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
L. ellipsostomus													
Edinburgh; Bogotá, Colombia	4	9.6	8.9–10.2	0.31	20.2	17.3–23.1	1.22	0.473	0.432–0.514	0.018	16.0	10.5–21.8	2.68
Edinburgh; Rio Solimoes, Brazil	4	9.1	8.8–9.2	0.10	18.5	17.8–18.9	0.26	0.489	0.476–0.497	0.005	18.1	14.2–21.0	1.73
L. diminutus													
MCZ 139832; Chanchamayo, Peru	12	13.0	12.2–13.8	0.14	27.7	26.5–28.9	0.24	0.469	0.443–0.496	0.005	9.1	7.6–12.4	0.41
ex MCZ 74750; Ucayali, Peru	5	10.1	9.4–10.6	0.22	23.0	21.5–25.1	0.68	0.437	0.387–0.474	0.015	11.4	6.2–17.0	1.74
CNHM 53634; Boca Inambari, Madre de Dios, Peru	4	10.9	10.8–11.0	0.05	27.3	26.2–28.8	0.59	0.400	0.375–0.420	0.010	8.2	6.7–10.0	0.70
L. tarapotoensis baeri													
CNHM 30049; Cerro Azul, Rio Ucayali, Peru	5	18.2	16.7–19.5	0.62	41.8	38.9–43.3	0.86	0.437	0.386–0.473	0.014	12.6	11.5–13.9	0.40
L. furcillatus													
MCZ 146119; Rio Paraná-Pura, Brazil	5	18.9	15.8–20.7	1.00	42.5	35.4–46.9	2.04	0.445	0.424–0.457	0.006	12.6	10.9–15.7	0.88

larger palatal teeth and a more open umbilicus, but otherwise is quite similar.

The locality "Sagarmo" could not be found on any map available to me, but is presumed to be near Perené, Dept. Junín. Preston's species is poorly figured, but the types show no characters separating them from the types of *diminutus*. The slightly larger basal tooth and bigger shell are not significant differences. Size variation in the Boca Inambari set is summarized in Table VII.

Several sets in older collections labeled as *yatesii* (=*ellipsostomus*) were transferred to *diminutus*. The differences are primarily in the thicker, less sharply carinated shell, generally larger size and heavier teeth of *diminutus*. The differences are of degree rather than kind and the relationship of *ellipsostomus* and *diminutus* needs considerable study.

The single Brazilian shell (USNM 171453) was collected by Garbe in 1902 from an unknown locality on the Juruá River. Shape, tooth size and degree of carination are as in *diminutus* rather than *ellipsostomus*.

Labyrinthus pronus Pilsbry, 1932. Figure 20a–b.

Labyrinthus pronus Pilsbry, 1932, Proc. Acad. Nat. Sci., Philadelphia, **84**, pp. 389–390, pl. 28, figs. 1,a,b—Uctubamba (*sic*), Dept. Libertad (error?), Peru at 7,000 feet elevation (M. A. Carriker!).

Pleurodonte (*Labyrinthus*) *baeri diminuta* Haas, 1947 (not Gude, 1903), Fieldiana: Zool., **31** (22), pp. 172–173—Yarinacocha, near Pucalpa, Loreto, Peru at 160 meters elevation (Schunke!).

Range.—Peru, Libertad and Loreto.

Material.—Peru: LORETO—Lago Yarina—Cocha, near Pucalpa at 160 meters elevation (CNHM 25867); Doma Santa Clara, 6° 55′ S, Ucayali River Valley (USNM 601377). SAN MARTÍN—Utcubamba (ANSP 159896 type).

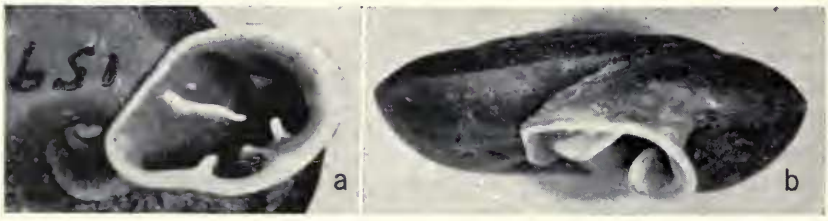


FIG. 20. *Labyrinthus pronus*, Utcubamba, 7,000 feet, Peru, ANSP 159896. Holotype. *a*, base; *b*, side.

Remarks.—Despite the difference in elevations and Utcubamba being located high above the Rio Huallaga while Pucalpa is on the Rio Ucayali, these appear to be the same species. The very flat spire, sharp angulation to the periphery, white lip and more strongly developed teeth separate the shells from *L. raimondii* and *L. diminutus*. The Yarinococha shells are more elevated than the type, but otherwise are quite similar. Possibly *L. diminutus* is only subspecifically separable.

Labyrinthus leprieurii (Petit, 1840). Figures 16b–d, 17a–d.

Helix Le Prieurii Petit, 1840, Revue Zool., **1840**, p. 74—French Guiana.

Helix leprieurii Petit, 1841, Guerin's Magazin de Zool., **1841**, pl. 32; Pfeiffer, 1848, Monog. helic. viv., **1**, p. 400; Reeve, 1852, Conch. Icon., *Helix*, pl. 10, fig. 560; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 462.

Helix auriculina Petit, 1840, Revue Zool., **1840**, p. 74—French Guiana; Petit, 1841, Guerin's Magazin de Zool., **1841**, pl. 33; Pfeiffer, 1848, Monog. helic. viv., **1**, p. 400; Pfeiffer, 1852, Syst. Conch. Cab., I (12), **2**, pp. 207–208, pl. 105, figs. 5–7; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 462.

Helix bifurcata Reeve, 1852 (not Deshayes, 1838), Conch. Icon., *Helix*, pl. 100, fig. 554—(French) Guiana.

Helix (*Labyrinthus*) *leprieurii* Petit, Pilsbry, 1895, Man. Conch. (2), **5**, pl. 174, pl. 40, figs. 96–99.

Pleurodonte (*Labyrinthus*) *leprieurii* (Petit), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95.

Range.—"French Guiana" and two localities in Peru.

Material.—French Guiana: No exact locality (CNHM 40763, CNHM 40766, Zurich, Edinburgh, ANSP 33174, ANSP 33175, ANSP 63581). *Peru:* LORETO—Doma Santa Clara, Ucayali River, 6° 55′ S (USNM 601357); SAN MARTÍN—Moyobamba (CNHM 40775, SMF 26379); Rio Huallaga (ZMA, Bartlett! 1867).

Diagnosis.—The very sinuately twisted parietal lamella comes directly off the parietal lip; basal lip strongly sinuated with one large, broad knob; lower palatal wall with a large, slightly subequally bifid tooth, narrower upper portion slanted upward; aperture very strongly deflected; parietal and basal lips slightly to strongly deflected into umbilicus; periphery right angled or acutely angulated; spire moderately to strongly elevated; color brownish, usually with a yellowish-white peripheral band. Diameter 18.9–26.2 mm., H/D ratio 0.445–0.558.

Remarks.—The nominate form has the lower palatal lip strongly indented at the bifid tooth, the basal and parietal lips deflected into the umbilicus, and is slightly larger (diameter 20.4–26.2 mm.); form

auriculina has the outer palatal margin rounded, the basal and parietal lips only slightly deflected into the umbilicus, and is smaller (diameter 18.9–21.8 mm.). Except for the new Peruvian records, only specimens from old collections could be located. Considerable variation in apertural outline exists, but in the total absence of distributional information its meaning cannot be assessed. The names *auriculina* and *leprieurii* recognized, respectively, the absence (fig. 16d) or the presence (fig. 16c) of a marked flattening or indentation of the lower palatal lip. More striking is the degree to which the parietal and basal lips converge to become parallel and dip into the umbilicus (fig. 16b–d). The degree of change is very large, but intermediate conditions are present. The Loreto shells have the indented lower palatal lip of *leprieurii*, but the basal and parietal lips of *auriculina*, while the Moyobamba shell is typical *auriculina*.

The original locality ("French Guiana") is probably erroneous.

Labyrinthus tarapotoensis tarapotoensis (Moricand, 1858). Figures 21b, 22a.

Helix tarapotoensis Moricand, 1858, Rev. et Mag. de Zool., **1858**, p. 450, pl. 13, fig. 2—Tarapoto, Peru; Pfeiffer, 1868, Monog. helic. viv., **5**, pp. 411–412; Pfeiffer, 1876, *Ibid.*, **7**, p. 462.

Helix (*Labyrinthus*) *tarapotoensis* Moricand, Pilsbry, 1889, Man. Conch. (2), **5**, p. 170, pl. 64, figs. 17–18.

Pleurodonte (*Labyrinthus*) *dacostiana* Haas, 1949 (not Preston, 1907), Fieldiana: Zoology, **31** (28), p. 236—Divisoria, Cerro Azul, Huanaco, Peru at 5,000 feet elevation (Schunke!).

Range.—Known from scattered localities in the Río Marañón, Putumayo, Río Mayo and Río Ucayali basins in Amazonian Peru.

Material.—Peru: SAN MARTÍN—Moyobamba (MCZ 87651). LORETO—Aguaitia River (=Aguanaitia?), Ucayali at 300 meters elevation (MCZ 159187). HUANACO—Divisoria, Cerro Azul, near Loreto border at 5,000 feet elevation (CNHM 30047, CNHM 30048). AMAZONAS—Balsas, Río Marañón (USNM 116888).

Remarks.—The white lip, obtusely angulated periphery, open umbilicus and prominent teeth are the main characters separating this from the other species. The seven specimens show comparatively little variation in size, shape or apertural armature. Compared with *L. t. baeri*, the teeth are smaller and more sharply outlined, the umbilicus slightly more widely open, and the shell smaller and more elevated.

Labyrinthus tarapotoensis baeri Dautzenberg, 1902. Figures 21c, 22b.

Helix (*Labyrinthus*) *baeri* Dautzenberg, 1902, Jour. de Conchy., **49** (4), pp. 306–307, pl. 9, figs. 1–3—Río Mixiollo, Huallaga, Peru (Baer!).

Pleurodonte (*Labyrinthus*) *baeri* Dautzenberg, Haas, 1949, Fieldiana: Zool., **31** (28), p. 235—Cerro Azul, Río Ucayali, near Contamana, Loreto, Peru.

Range.—Huallaga and Ucayali River basins in San Martín and Loreto, Peru.

Material.—Peru: SAN MARTÍN—Huallaga District (ANSP 131428). LORETO—Cerro Azul, near Contamana (CNHM 30049, MCZ 159188, ANSP), Doma Santa Clara, 6° 55′ S, Ucayali Valley (USNM 601370).

Remarks.—The enlarged parietal tooth running into or near to the lip, obtusely angulated periphery, somewhat smaller umbilicus and white lip are the characters separating *L. t. baeri* and *L. raimondii*. Differences from *L. t. tarapotoensis* are given in the discussion of that form. The three known localities are far apart, the Río Mixiollo being a western tributary of the Río Huallaga; the Cerro Azul lying on the east bank of the Río Ucayali above Contamana, and Santa Clara lying downstream from Contamana. The specimens from Cerro Azul have the parietal lamella a little shorter and the periphery slightly more sharply angulated than in the figures of the type. They are also slightly smaller. Size variation is summarized in Table VII. The two examples from Doma Santa Clara were dead when collected. They are quite distinctive in having a very sinuated basal lip and deeply indented lower palatal lip. The lip form is very close to that seen in *L. leprieurii* (see fig. 16), although the parietal lamellae and lips are totally different. The effect of the lip sinuosity is to decrease the apertural opening, thus presumably lessening the chance of predation. It is impossible to be certain that the Doma Santa Clara shells actually are *baeri*, but they are nearest to this morph.

Labyrinthus raimondii (Philippi, 1867). Figures 21d, 22c.

Helix raimondii Philippi, 1867, Malak. Blätt., **14**, p. 65—between Santa Catalina and Yanayaco, Dept. Loreto, Peru; Pfeiffer, 1867, Novit. Conch., **3**, pp. 329–330, pl. 79, figs. 7–9; Hidalgo, 1869, Viage al Pacifico, Moll., p. 17, pl. 2, figs. 4–5—Napo, Ecuador; Pfeiffer, 1876, Monog. helic. viv., **7**, pp. 461–462.

Labyrinthus raimondii (Philippi), Miller, 1878, Malak. Blätt., **25**, p. 167; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 64—Napo.

Helix (*Labyrinthus*) *raimondii* Philippi, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 172–173, pl. 40, figs. 91–95.

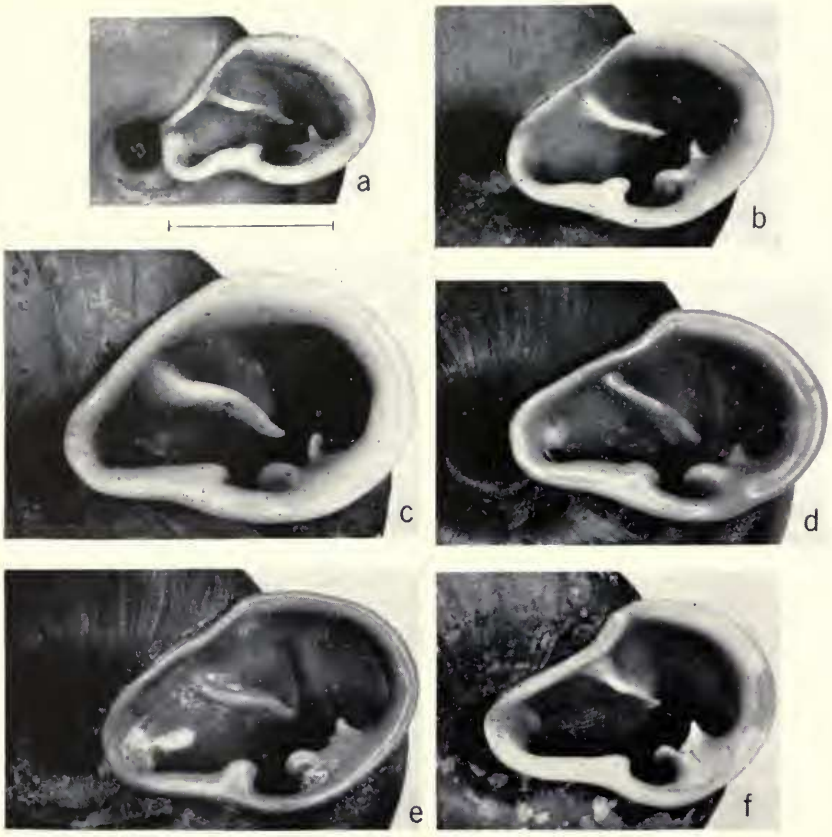


FIG. 21. Apertures of: *a*, *Labyrinthus diminutus*, Perené, Junín, Peru. Edinburgh. Lectotype; *b*, *Labyrinthus tarapotoensis*, Divisoria, Cordillera Azul, Peru, CNHM 30047; *c*, *Labyrinthus t. baeri*, Cerro Azul, Río Ucayali, Peru, CNHM 30049; *d*, *Labyrinthus raimondii*, Napo River Valley, Ecuador, CNHM 117841; *e*, *Labyrinthus furcillatus*, "Ecuador," CNHM 132549; *f*, *Labyrinthus bifurcatus*, "Quito, Ecuador," CNHM 40765. Scale line equals 10 mm.

Pleurodonte (*Labyrinthus*) *fragilis* Haas, 1949, Arch. f. Mollusk., **78** (4-6), p. 155, pl. 7, fig. 3—forest near Belterra, Lower Rio Tapajóz, Brazil (Sioli!).

Pleurodonte (*Labyrinthus*) *manuelis* (*sic*) Haas, 1955 (not Higgins, 1872), Fieldiana: Zool., **34** (35), p. 368—Rio Ucayali, near Pucalpa, Dept. Loreto, Peru at 200 meters elevation (Schunke!).

Range.—Amazonian basin from Amazonas and Caquetá in Colombia to southern Loreto in Peru and the Río Tapajóz in Pará, Brazil. There are two records from the Río Esmereldas drainage on the Pacific slopes of the Ecuadorean Andes (Mindo and Santo Domingo de los Colorados).

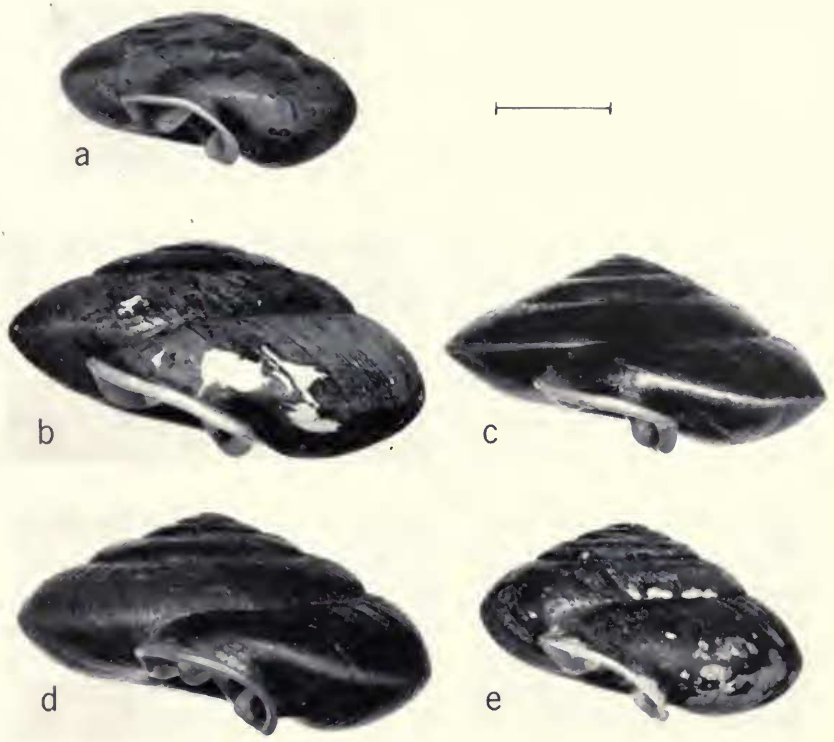


FIG. 22. Shells of: *a*, *Labyrinthus tarapotoensis*, Divisoria, Cordillera Azul, Peru, CNHM 30048; *b*, *Labyrinthus t. baeri*, Cerro Azul, Río Ucayali, Peru, CNHM 30049; *c*, *Labyrinthus raimondii*, Napo River Valley, Ecuador, CNHM 117841; *d*, *Labyrinthus furcillatus*, "Ecuador," CNHM 132549; *e*, *Labyrinthus bifurcatus*, "Quito, Ecuador," CNHM 40765. Scale line equals 10 mm.

Material.—Normal form. *Peru:* LORETO—Yurimaguas, Río Mayo (CNHM 40759); Alto Yavari, zone of mouth of Río Yaquerana (CNHM 67593); Contamana at 160 meters (SMF 141097); near Pucalpa, Río Ucayali at 200 meters elevation (CNHM 30703); Borja, Río Marañón (CNHM 95655); Alto Amazonas, Río Morona, mouth of Río Amayo (CNHM 67892). *Ecuador:* No exact locality (Zurich, Edinburgh, CNHM 251, CNHM 100133); Nachiyacu (ANSP 170705, Jackson 4715); Napo (Jackson 5296, MCZ 92315, CNHM 86696, CNHM 117839); Napo River Valley (CNHM 117841); Sarayaco, Río Bobonaza at 400 meters (SMF 156309); Chicherota, Bobonaza River, Pastaza River (ANSP); Puyo at 1,000 meters elevation (CNHM 117838); Mindo (Jackson 4814); Jatamyacu at 700 me-

ters (CNHM 117840, MCZ 64956); Mera (Jackson 5518); Milpe (Jackson 4819); Santo Domingo de los Colorados (Jackson 9745). *Colombia:* PUTUMAYO—La Tagua (SMF 162666); Puerto Leguizamo (CNHM 114002); Río Mecaya, tributary of Upper Caquetá River (CNHM 114000); Las Lomitas, Río Sencella, Upper Caquetá River (CNHM 114001); CAQUETÁ—Cano La Duche, abajo de la Colonia de Araracuara (CNHM 114107); El Salado, below Curiplaya, Upper Caquetá River (CNHM 114143). *Brazil:* PARA—Belterra, Río Tapajóz (CNHM 30399, holotype of *fragilis* Haas).

Dwarf form. *Peru:* LORETO—Río Samaria, Santa Elena, Iquitos at 130 meters elevation (CNHM 64407); Río Nanay, Santa Luisa, Iquitos at 160 meters elevation (CNHM 64406); Pucalpa, Rio Ucayali at 200 meters elevation (CNHM 47099); Colonia Calleria, Río Calleria, 15 km. from Ucayali (CNHM 114186). *Brazil:* PARA—Ford's Rubber Plantation, Río Tapajóz, Bon Vista (ANSP 166721).

Remarks.—The acutely angulated to carinated periphery and brownish tone of the lip and teeth are the main identifying characters. In *pronus* the spire is flatter, the lip white, and the basal lip seemingly more sinuated, while in *diminutus* the shell is small, less carinated and the lip is white. *L. furcillatus* differs only in having the two arms of the lower palatal lamella farther apart. It probably is not specifically distinct, but in the absence of localized material is separated.

The original specimens of *raimondii* from near Yanayacu on the Bajo Ucayali and those reported by Hidalgo (1869) from "Napo," Ecuador were quite large, diameter 45 and 51 mm., respectively. Of the modern specimens, only a few shells reach this size. Most are between 35.5–43.4 mm. in diameter. However, five "dwarf" specimens are 22.4–28.2 mm. in diameter. An interesting set of four specimens (CNHM 67892 from Alto Amazonas, Rio Morona, mouth of Río Amayo, Dept. Loreto) has diameters of 31.8, 35.8, 41.8 and 41.9 mm., indicating the extent of size variation. The two larger shells have the parietal lip only slightly free of the wall and the outer palatal lip slightly sinuated, while in the two smaller the parietal lip is further removed from the wall and the lower palatal lip becomes progressively more sinuated. The largest shell has the spire evenly elevated with flatter sides, while the three smaller have less elevated spires with rounded sides. No separation into two forms is possible, since intermediate conditions can be found among most of the other available specimens. Another slight variation is seen in a small set

TABLE VIII.—Size and shape variation in *Labyrinthus raimondii*, *L. clappi*, *L. otostomus bogotensis* and *L. creveauxianus*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
L. raimondii													
CNHM 67892; Rio Morona, Loreto, Peru	4	15.0	11.8–17.0	1.16	38.6	31.8–44.8	2.94	0.393	0.371–0.421	0.012	7.5	6.36–9.29	0.63
Jackson 4814; Mindo, Ecuador	4	16.8	15.7–17.9	0.50	40.5	37.8–43.8	1.25	0.415	0.358–0.441	0.020	8.3	6.3–10.5	0.86
Jackson 5296; Napo, Ecuador	7	17.0	15.8–18.1	0.27	40.6	36.4–44.6	1.43	0.419	0.374–0.466	0.012	8.2	7.0–9.7	0.34
Jackson 5518; Mera, Ecuador	40	17.9	14.4–20.8	0.26	42.0	36.1–48.8	0.61	0.427	0.384–0.486	0.003	8.2	6.8–9.8	0.11
Jackson 4819; Milpe, Ecuador	3	17.3	16.5–18.2	0.49	42.1	40.6–43.0	0.77	0.413	0.386–0.429	0.013	7.1	6.9–7.3	0.12
L. clappi													
CM 62.16585 and CM 4531; Los Nubes, Colombia	7	19.4	17.7–20.7	0.37	32.8	30.6–34.5	0.53	0.594	0.554–0.648	0.012			
L. otostomus bogotensis													
ANSP 174437 and MCZ 64931; Muzo, Colombia	5	14.6	13.6–15.9	0.47	33.7	31.3–38.3	1.25	0.434	0.415–0.454	0.001	10.4	8.1–12.3	0.80
L. creveauxianus													
Edinburgh; Frontino, Colombia	5	14.6	14.2–14.8	0.12	35.5	35.1–35.9	0.16	0.409	0.397–0.420	0.004	10.6	8.0–13.0	0.87
CNHM 248; "Ecuador"	5	14.1	13.4–14.9	0.24	34.4	33.1–36.1	0.48	0.411	0.371–0.433	0.011			

(3 examples) from the Río Yaquerana on the Peruvian–Brasilian border (CNHM 67593). Here the parietal lip is much more accentuated and free of the penultimate whorl, the parietal lamella is longer and slightly sinuated, and only one of the three specimens shows a trace of brownish cast to the lip. The diameters are 34.6, 36.8, and 43.3 mm. This is the only set tending toward the *baeri* type. In some of the smaller specimens the aperture is rather constricted by the presence of an inward sinuation of the lower palatal lip, much as in the typical form of *L. leprieurii.*

The five specimens from Loreto and Pará referred to as a "dwarf form" are quite interesting. Not only are they much smaller (see Table VII), but their D/U ratio is larger than in the normal forms. In the latter the distribution of the D/U ratio is:

Ratio	6.2	6.7	7.2	7.7	8.2	8.7
Number of examples	2	5	9	22	24	21
Ratio	9.2	9.7	10.2	10.7	11.2	11.7
Number of examples	14	8	4	2	1	1

In tooth structure, color, shape and spire, the smaller shells do not differ significantly from the larger. Possibly they represent a dwarf ecological form.

The holotype of *L. fragilis* Haas is a very thin, probably subadult shell. Its moderately open umbilicus (D/U ratio 10.2) probably is caused by the subadult lip condition. It is, however, within the range of variation of normal *raimondii.* Similarly, the diameter (37.3 mm.) is not unusual. The H/D ratio (0.502) is large, but not beyond the known range of variation. In view of the fact that the other shell from Pará (ANSP 166721) is the dwarf form of *raimondii,* synonymization of *fragilis* and *raimondii* seems probable.

Labyrinthus furcillatus (Hupé, 1853). Figures 21e, 22d.

Helix furcillata Hupé, 1853, Rev. et Mag. de Zool., **1853**, pp. 302–303, pl. 11, fig. 2—Huancavelica, Peru; Pfeiffer, 1855, Novit. Conch., **1**, pp. 58–59, pl. 17, figs. 3–4 ("*H. erecta*" on plate caption)—Meobamba, Peru (Yates!); Hupé, 1857, *in* Castelnau's Exped. Amer. Sud., Moll., pp. 18–19, pl. 3, fig. 1; Pfeiffer, 1859, Monog. helic. viv., **4**, pp. 304–305; Pfeiffer, 1876, *Ibid.*, **7**, p. 462.

Helix (*Labyrinthus*) *furcillata* Hupé, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 171–172, pl. 39, figs. 91–92.

Labyrinthus furcillatus (Hupé), Miller, 1878, Malak. Blätt., **25**, p. 167; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 63.

Range.—Peru, San Martín and Huancavelica.

Material.—"Amazone" (USNM 515467); "Peru" (ANSP 113573, Edinburgh); "Ecuador" (Zurich, CNHM 132549); "Paraná-Pura" (MCZ 146119); "Tarapoto, Peru" (SMF 172170); "New Granada" (SMF 172172); "Pebas, LORETO" (SMF 172161).

Remarks.—The white to brownish lip, rounded or obtusely angulated periphery and open umbilicus are as in *L. tarapotoensis*. The main difference lies in *furcillatus* having the two arms of the bifurcated lower palatal tooth widely separated, while in *tarapotoensis* and *raimondii* they are much closer together. The constancy and importance of this character are unknown. The only known records of this species date from the 1850's, and no reliable locality records exist.

Labyrinthus bifurcatus (Deshayes, 1838). Figures 21f, 22e.

Helix bifurcata Deshayes, 1838, Guerin's Magasin de Zool., **1838**, class 5, pl. 111, fig. 2; Pfeiffer, 1848, Monog. helic. viv., **1**, p. 379; Pfeiffer, 1852, Syst. Conch. Cab., I (12), **2**, p. 207, pl. 105, fig. 1; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 305—Meobamba, Peru; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 462.

Helix (*Labyrinthus*) *bifurcata* Deshayes, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 170–171, pl. 64, figs. 22–23.

Range.—Unknown.

Material.—*Ecuador:* "Quito" (CNHM 40765). "New Granada" (Edinburgh, Zurich).

Remarks.—The original specimen was probably subadult and is from an unknown locality. The white lip, obtusely rounded periphery and partially obscured umbilicus are the main characters of this form. The size of the type is diameter 37 mm., height 15 mm.

No accurately localized examples were seen. It may be that this species is based on extreme variants of *furcillatus* or *tarapotoensis*. The few examples located were all small, diameter 29.4–34.5 mm. (mean 31.4 mm.), with rather markedly elevated spire, H/D ratio 0.432–0.545 (mean 0.508).

Group of *Labyrinthus aenigmus*

The species grouped here show more geographical unity than morphologic identity. Except for *L. clappi* Pilsbry from the Sierra Nevada de Santa Marta, they are known only from the Cauca, Atrato and Magdalena River basins north of 5° N. latitude. *L. o. assimilans* and *L. o. otostomus* have not been reported from an exact locality, and the others are known from only a single locality or from plantations

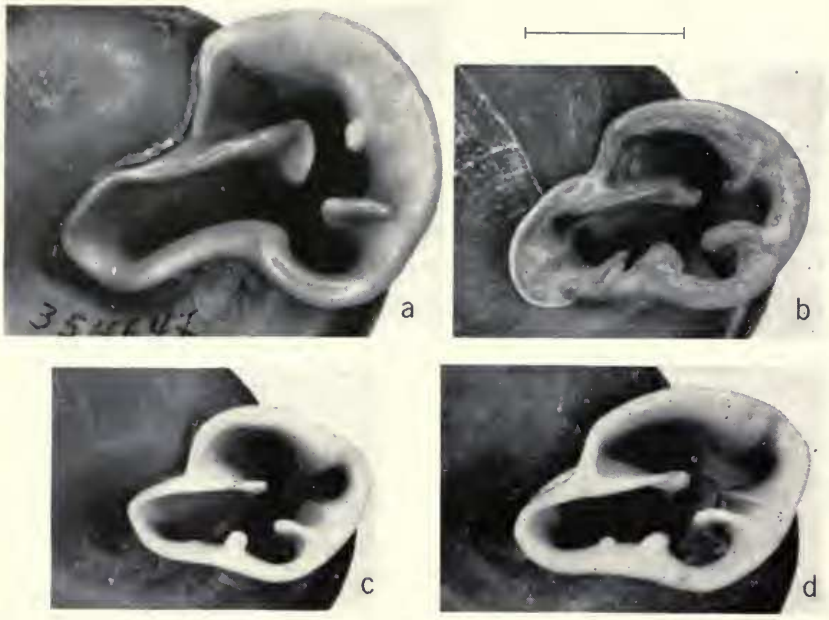


FIG. 23. Apertures of: *a*, *Labyrinthus aenigmus*, no locality, USNM 354647; *b*, *Labyrinthus clappi* Los Nubes Estate, 5,000 feet elevation, Sierra Nevada de Santa Marta, Colombia, CNHM 132086; *c*, *Labyrinthus o. otostomus*, Colombia. Edinburgh; *d*, *Labyrinthus o. bogotensis*, "New Granada," CNHM 40758. Scale line equals 10 mm.

within a limited geographic area. The imperforate *L. clappi* does not have the lower parietal lip fused with the parietal lamella, while the other species have the type of fusion found in *L. manueli*, *L. vexans* and *L. magdalenensis*. *L. aenigmus* has a nearly closed umbilicus, very sinuated twisted basal lip and strong palatal teeth, but no basal tooth. The very closely related *L. o. bogotensis*, *L. o. otostomus* and *L. o. assimilans* have a double lower palatal tooth that is unique in having the two arms parallel rather than diverging as in the *raimondii* series.

Gude (1912) proposed a new genus, *Ambages* (type species: *Helix vexans* Dohrn, 1875 by original designation), for *L. vexans*, *L. aenigmus*, *L. assimilans* and *L. sharmani*. *Ambages* was characterized by the teeth being more developed than in *Isomeria* and the shell more sub-globose than in *Labyrinthus*. The shell shape is not importantly different and *L. vexans*, the type species of *Ambages*, is separable only with great difficulty from several species of *Labyrinthus*. A better

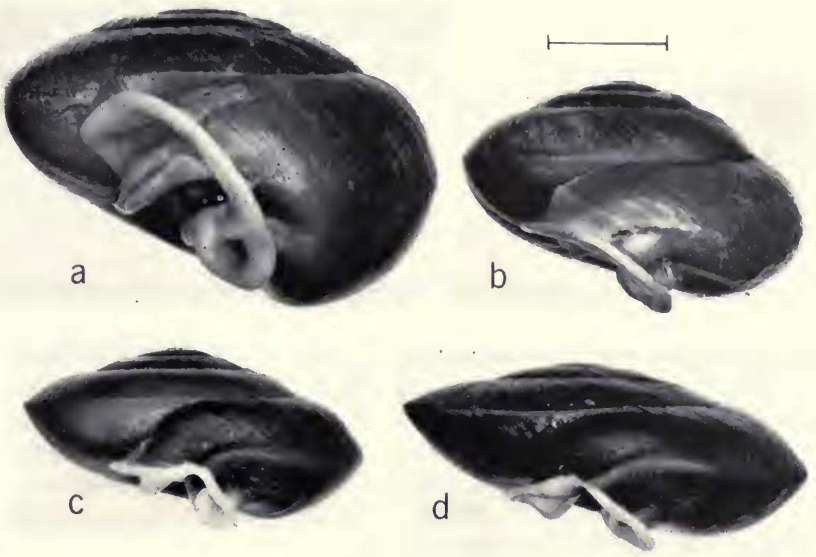


FIG. 24. Shells of: *a*, *Labyrinthus aenigmus*, no locality, USNM 354647; *b*, *Labyrinthus clappi*, Los Nubes Estate, 5,000 feet elevation, Sierra Nevada de Santa Marta, Colombia, CNHM 132086; *c*, *Labyrinthus o. otostomus*, Colombia. Edinburgh; *d*, *Labyrinthus o. bogotensis*, "New Granada," CNHM 40758. Scale line equals 10 mm.

case could have been made for separation of *L. aenigmus* and *L. clappi*, but *L. vexans* is nearly typical *Labyrinthus*.

KEY TO THE *LABYRINTHUS AENIGMUS* GROUP

1. Umbilicus at least partly open.....2
   Umbilicus completely closed.....*Labyrinthus clappi* Pilsbry, 1901
2. Lower palatal lip with 2 parallel lamellae or one lamella with a strong upper buttress.....3
   Lower palatal lip with one lamellar tooth.
   Labyrinthus aenigmus (Dohrn, 1875)
3. Basal lip with two teeth.....4
   Basal lip with one tooth.....*Labyrinthus o. otostomus* (Pfeiffer, 1852)
4. Periphery acutely carinated; diameter 37 mm.
   Labyrinthus o. bogotensis (Pfeiffer, 1854)
   Periphery nearly a right angle; diameter 26 mm.
   Labyrinthus o. assimilans Smith, 1897

Labyrinthus aenigmus (Dohrn, 1875). Figures 23a, 24a.

Helix (*Isomeria*) *aenigma* Dohrn, 1875, Jahrb. deutsch. Malak. Gesell., 2, pp. 292–294, pl. 10, figs. 1–2—Frontino, Antioquia, Colombia at 6,000 feet

elevation; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 591; Dohrn, 1886, Syst. Conch. Cab., I (12), **4**, pp. 625–626, pl. 180, figs. 1–2; Pilsbry, 1889, Man. Conch. (2), **5**, p. 158, pl. 39, figs. 93–94, pl. 44, figs. 1–2.

Pleurodonte (*Isomeria*) *aenigma* (Dohrn), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Known only from the type collection.

Material.—"New Granada" (ANSP 30647, MCZ 74568, USNM 354647, Zurich). *Colombia:* ANTIOQUIA—Frontino (Zurich, paratypes).

Diagnosis.—The parietal lamella is high and continuous with the moderately elevated lower parietal lip (which is much lower than the lamella), while the upper parietal lip is greatly reduced in prominence and inserts perpendicularly into the lamella; the basal lip is very sinuated and has a strong terminal swelling, but is not toothed; the lower palatal lip has a prominent crescentic lamella twisted inward posteriorly; upper palatal lip with a lower, broadly rounded lamella; umbilicus nearly closed by basal and parietal lips; periphery angulated at nearly 90°. Diameter 46–49 mm. (mean 46.9 mm.), H/D ratio 0.497–0.550 (mean 0.522).

Remarks.—The absence of the basal tooth, very sinuated basal lip, much larger size and strongly angulated periphery easily separate *aenigmus* from *vexans*, which has a nearly straight basal lip with two teeth, a much more open umbilicus and the lower parietal lip is not reduced in height.

The only known locality is Frontino, all museum material being either paratypic or from "New Granada."

Labyrinthus clappi Pilsbry, 1901. Figures 23b, 24b.

Pleurodonte (*Labyrinthus*) *clappi* Pilsbry, 1901 (July), Nautilus, **15** (3), pp. 34–35, pl. 2, figs. 3–4—Alto de Cielo, 5,000 feet elevation, Sierra de Santa Marta, Magdalena, Colombia in forest among rotting leaves on ground.

Labyrinthus colombiensis Da Costa, 1901 (December), Ann. Mag. Nat. Hist. (7), **8**, pp. 557–558, 2 figs.—Santa Marta, Colombia.

Range.—Colombia, Sierra Nevada de Santa Marta, probably at higher elevations only.

Material.—*Colombia* (Edinburgh): MAGDALENA—Sierra Nevada de Santa Marta (CNHM 40771, USNM 307449); Los Nubes Estate, Sierra Nevada de Santa Marta at 4,000 feet (CM 62.16585, USNM 171917, CNHM 132086); Don Amo Estate, 4,000 feet elevation, Sierra Nevada de Santa Marta (ANSP 83168, CM 4530); Alto de Cielo, Sierra Nevada de Santa Marta, 5,000 feet elevation (CM 4091).

Diagnosis.—The sinuated parietal lip is appressed to the wall with a thick raised edge; high curved parietal lamella descending to join edge of lower portion of the parietal callus; basal lip nearly straight with two very prominent thick lamellae; lower palatal wall with single high, crescentic lamella twisted slightly downward; upper palatal wall with a smaller conical lamella twisted slightly upward, laterally buttressed; umbilicus completely closed; periphery obtusely angulated, with slight keel. Diameter 30.6–34.5 mm. (mean 32.9 mm.), H/D ratio 0.554–0.648 (mean 0.595).

Remarks.—The completely closed umbilicus, very prominent teeth and appression of the parietal lip to the wall easily separate *L. clappi* from other *Labyrinthus*. The only other species with closed umbilicus, *L. sieversi* (Martens) also from the Sierra Nevada de Santa Marta, has a less sinuated parietal lip that the parietal lamella fails to reach, quite differently constructed palatal teeth, and is much, much smaller (diameter 17.4–19.0 mm.). I doubt that *clappi* and *sieversi* will be found to be very closely related. Probably they were separately derived from the *isodon* complex.

All known localities for *L. clappi* are from the rather isolated northwest spur of the Sierra Nevada. Both Don Amo Estate and Los Nuves (=Los Nubes) are on the north face of the spur below the peak named La Horqueta. The known altitudes of 4,000–5,000 feet are well below the apparent habitat of the new species *Isomeria medemi* (see p. 00) that has recently been collected at 8,200 to 8,850 feet on the San Lorenzo ridge in the same mountain mass. *L. sieversi* has been collected only on the north face and the northeast spur of the main mass of the Sierra Nevada de Santa Marta.

Labyrinthus otostomus otostomus (Pfeiffer, 1852). Figures 23c, 24c, 25a.

Helix stostoma (*sic*) Pfeiffer, 1852, *in* Reeve's Conch. Icon., *Helix*, pl. 100, fig. 551—Andes of Colombia.

Helix otostomus Pfeiffer, 1853, Proc. Zool. Soc. London, **1851**, p. 260; Pfeiffer, 1853, Monog. helic. viv., **3**, pp. 255–256.

Helix (*Labyrinthus*) *otostoma* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 176, pl. 64, fig. 29.

Pleurodonte (*Labyrinthus*) *otostoma* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 96.

Range.—Unknown.

Material.—*Colombia* (Edinburgh).

Diagnosis.—The high parietal lamella is continuous with the elevated lower lip, while the upper parietal lip is greatly reduced in size

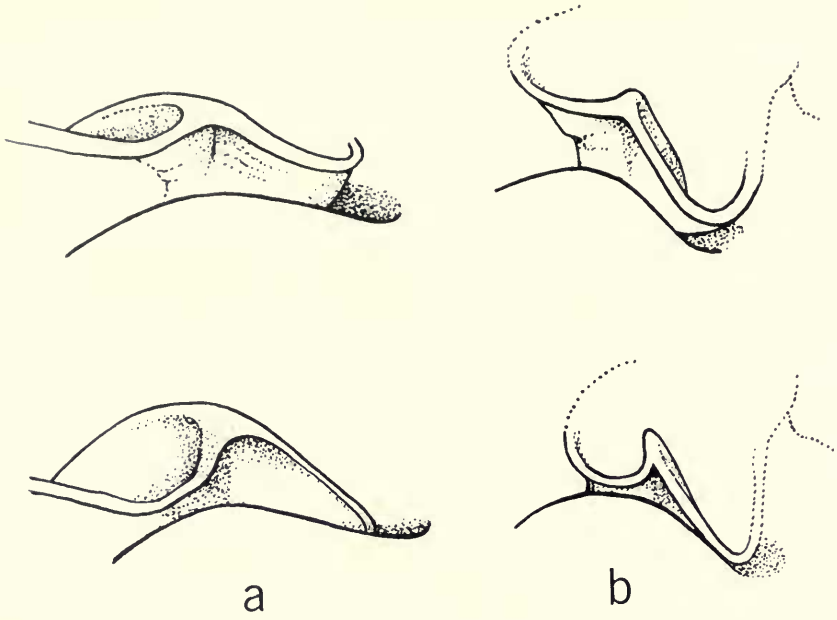


FIG. 25. Parietal lips in *Labyrinthus o. otostomus* and *Labyrinthus o. bogotensis*: *a*, *Labyrinthus o. otostomus*; *b*, *Labyrinthus o. bogotensis*.

and inserts onto the lamella at a nearly perpendicular angle; basal lip moderately sinuated with one prominent crescentic lamellar tooth and a trace of an inner tooth; lower palatal lip with two closely set teeth as in *bogotensis*, upper reduced to forming edge to callus; upper palatal wall with a single triangular supraperipheral tooth; umbilicus moderately open; periphery acutely carinated. Diameter 32 mm., H/D ratio 0.477.

Remarks.—*L. o. otostomus* is obviously very closely related to *L. o. bogotensis*. The comparatively minor differences are in the much greater reduction of the upper parietal lip and loss or very great reduction of the inner basal tooth in *L. o. otostomus*. This subspecies has never been reported from an exact locality. *L. o. bogotensis* may be only an extreme variant.

Labyrinthus otostomus bogotensis (Pfeiffer, 1854). Figures 23d, 24d, 25b.

Helix bogotensis Pfeiffer, 1854, *in* Reeve's Conch. Icon., *Helix*, pl. 196, fig. 1381 —Santa Fe de Bogotá, Colombia; Pfeiffer, 1855, Proc. Zool. Soc. London, **1854**, p. 288; Pfeiffer, 1859, Monog. helic. viv., **4**, pp. 305–306.

Helix (*Labyrinthus*) *bogotensis* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 176, pl. 42, fig. 40.

Pleurodonte (*Labyrinthus*) *bogotensis* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 96.

Range.—Known only from the type locality.

Material.—*Colombia:* "New Granada" (CNHM 40758); Santa Fe de Bogotá (ANSP 33168, SMF, SMF 82536, ZMA, Edinburgh, paratypes); BOYACÁ—Muzo (ANSP 174437, MCZ 64931).

Diagnosis.—The parietal lamella is very high and continuous with the strongly elevated lower parietal lip, while the upper parietal lip is distinctly lower and slants into the lamella; basal lip slightly sinuated with two prominent teeth, inner smaller; lower palatal lip with two nearly parallel teeth set closely together and joined by a callus, upper tooth distinctly lower or reduced to forming edge of callus; periphery slightly reflected to form a weak spout with upper palatal margin extended inward to form a blunt triangular tooth; umbilicus slightly less than half closed by basal and parietal lips; periphery acutely carinated, spire somewhat flattened. Diameter 29.1–40.4 mm. (mean 35.1 mm.), H/D ratio 0.393–0.478 (mean 0.430).

Remarks.—The higher upper parietal lip and prominent inner basal tooth separate *bogotensis* from *otostomus*. The conical upper palatal tooth and two lower palatal teeth are the characters immediately separating it from *vexans* and *aenigmus*.

Labyrinthus otostomus assimilans E. A. Smith, 1897. Figure 26a–b.

Labyrinthus assimilans E. A. Smith, 1897, Jour. of Malac., **6** (2), p. 27, pl. 4, figs. 6–8—Cauca River, Colombia.

Range.—Known only from the type collections.

Diagnosis.—The parietal lamella is very high and continuous with the lower parietal lip, the upper lip being reduced in size; basal lip very slightly sinuated with two prominent teeth; lower palatal lip with two prominent, close-set teeth, upper distinctly smaller; periphery slightly reflected forming a spout with a small conical pointed tooth on the lower margin of upper palatal lip; umbilicus but slightly covered by basal and parietal lips; periphery nearly right angled. Diameter 26 mm.

Remarks.—According to Smith, this species is very near to *bogotensis*, but is "... much smaller (in) size and (with) much more obtuse periphery. The peristome also is not so produced or pointed in front,

the sinus between the tubercle within the upper margin and the large double tooth within the front margin being shallower and of a different form."

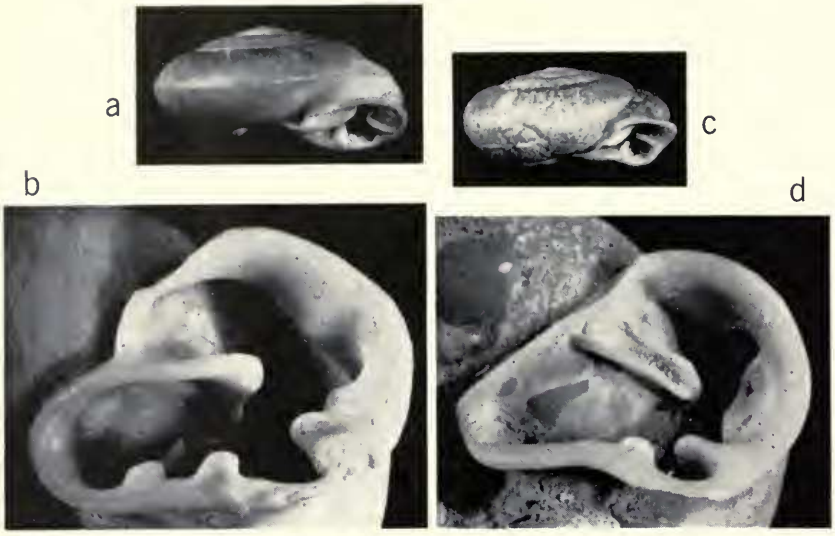


FIG. 26. Types from the British Museum: *a–b, Labyrinthus o. assimilans,* Cauca River, Colombia, BM(NH) 97.7.26.7–8 (*a,* side; *b,* aperture); *c–d, Labyrinthus sharmani,* Alejandría, Antioquia, Colombia, BM(NH) 1912.1.27.1 (*c,* side; *d,* aperture). Reproduced by permission of the British Museum (Natural History).

The two types in the British Museum (Natural History) (97.7.26. 7–8) are the only known examples.

Group of *Labyrinthus unciger*

The two species have one basal and one sinuated parietal lamella, a lower palatal lamella surmounted by a deeply recessed, hooked (usually) or "T"-shaped tooth, lenticular form and a protruded knife-edge peripheral keel. Form of the aperture and of the basal and parietal lamellae are readily derivable from members of the *isodon* complex. The unique structure of the palatal lamella with its entering ridge or callus and the posterior hooked tooth or "T"-shaped lamella seems to present no similarity with the structures found in other *Labyrinthus,* but could be derived from the palatal tooth type of *L. triplicatus.*

The smaller, spirally-color-banded *L. unciger* probably ranges from Limón, Costa Rica to somewhere in Chocó, Colombia at low to moderate elevations. The larger, unicolored *L. creveauxianus* is

known only from Frontino, Antioquia, Colombia. Possibly it may be found at higher elevations in Darién, Panama.

Species recognition is most easily accomplished by the presence of red spiral sub- and supra-sutural bands in *L. unciger* and the unicolor of *L. creveauxianus*. There are also structural differences, particularly in the curvature of the parietal lip (lower and outer edge concave in *unciger;* higher and outer edge straight or convex in *creveauxianus*), length of the parietal lamella (short of lip in *unciger;* running into lip in *creveauxianus*), and more rounded spire in *unciger*. In *creveauxianus* the tooth is a twisted, hooked structure usually without strong lateral supports, while in *unciger* it varies greatly (see fig. 29).

Labyrinthus unciger (Petit, 1838). Figures 27a–b, 29.

Carocolla uncigera Petit, 1838, Guerin's Mag. de Zool., **1838**, pl. 113—Panama (Pavageau!).

Helix uncigera (Petit), Pfeiffer, 1848, Monog. helic. viv., **1**, pp. 398–399; Deshayes, 1851, Hist. Nat. Moll., **1**, pp. 385–386, pl. 45B, figs. 2–3; Pfeiffer, 1852, Syst. Conch. Cab., I (12), **2**, p. 206, pl. 104, figs. 8–10 (plate issued in 1850); Reeve, 1852, Conch. Icon., *Helix*, pl. 100, fig. 552.

Helix (*Labyrinthus*) *uncigera* (Petit), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 164–165, pl. 42, figs. 23–26 (form *chiriquiensis* Pilsbry, 1910); Kobelt, 1893, Syst. Conch. Cab., I (12), **4**, p. 632, pl. 181, figs. 13–14.

Helix uncigera var. *conoidea* Ancey, 1890, Bull. Soc. Malac. France, **7**, p. 152—Colombia.

Helix uncigera var. *anopla* Ancey, 1890, *loc. cit.*, **7**, p. 152—Colombia.

Caracolla uncigera (Petit), Pilsbry, 1893, Man. Conch. (2), **8**, p. 264.

Pleurodonte (*Labyrinthus*) *tenaculum* Dall, 1909, Smith. Misc. Coll., **52** (3), pp. 361–362, fig. 64, pl. 37, figs. 5, 6, 10, 11—mountains of Atrato River, "Sierra Darién," Panama (A. E. Heighway!).

Pleurodonte (*Labyrinthus*) *uncigera* (Petit), Pilsbry, 1910, Proc. Acad. Nat. Sci., Philadelphia, **1910**, p. 506, fig. 1; Pilsbry, 1926, *op. cit.*, **78**, pp. 75–76, fig. 6c, pl. 9, fig. 6—Rio Puerco (=Pucro), Darién, Panama.

Pleurodonte (*Labyrinthus*) *uncigera chiriquiensis* Pilsbry, 1910, Proc. Acad. Nat. Sci., Philadelphia, **1910**, pp. 506–507, fig. 2—Chiriquí (Lagoon), Panama.

Pleurodonte (*Labyrinthus*) *chiriquiensis* Pilsbry, 1926, *op. cit.*, **78**, p. 76, fig. 6b, pl. 9, fig. 5.

Pleurodonte (*Labyrinthus*) *chiriquiensis* mutant *tau* Pilsbry, 1926, *loc. cit.*, **78**, p. 76, fig. 6a—Mono Creek, Almirante and Bocas del Toro Island (A. A. Olsson!).

Range.—Atlantic drainage of Panama from Costa Rica border to the lower reaches of the Atrato River basin in Colombia. Probably will be found in Limón, Costa Rica.

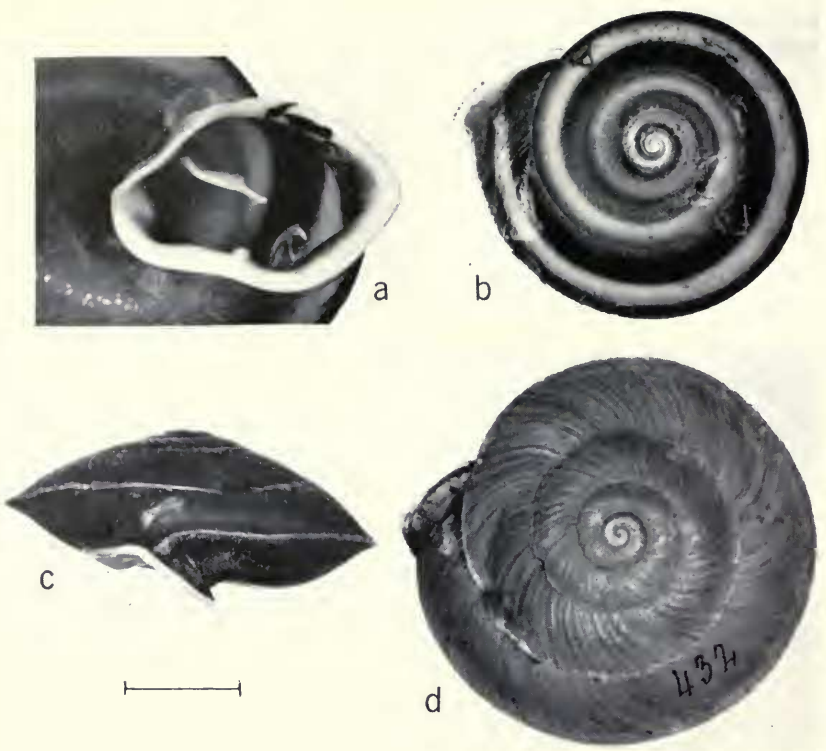


FIG. 27. Shells of: *a–b, Labyrinthus unciger* form *chiriquiensis*, Club Campestre, Panama, CNHM 73371 (*a*, base; *b*, side); *c–d, Labyrinthus creveauxianus*, Frontino, Colombia. Basel 432a. Lectotype (*c*, side; *d*, top). Scale line equals 10 mm.

Material.—Form *unciger*—*Colombia:* CHOCO—Arquía, 1½ hours' walk from Unguia (CNHM 113998, CNHM 114110); Acandi (ANSP 164970); Golfo de Urabá (R. Wright Barker); mountains near mouth of Atrato River (USNM 111073 types of *tenaculum* Dall, 1909). *Panama:* DARIEN—Rio Pucro (ANSP 140305). PANAMA—mountains around Gaspasalama, upper Mamoní River (USNM 228906); half way from Cerro Azul to Mandingo (ANSP 243693); Cerro Campana (MCZ, CNHM 132552). COMARCA DE SAN BLAS—Puerto Obaldia (USNM 228666). CANAL ZONE—No exact locality (USNM 225984); Río Pequení (MCZ 133476); Salamanca Hydrographic Station, Río Pequení at 300 feet elevation (MCZ 111174).

Form *tau*—*Colombia:* CHOCO—Acandi (USNM 341768). *Panama:* COLON—Río Salud (ANSP 155387, USNM 618724). COCLÉ

—El Valle (MCZ 88933). BOCAS DEL TORO—Mono Creek, Almirante (ANSP 140304); Bocas del Toro Island (ANSP 140303 types of *tau*).

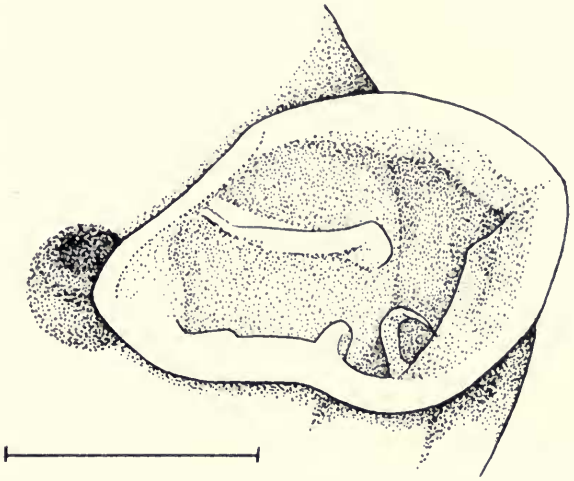


FIG. 28. Aperture of: *Labyrinthus creveauxianus*, Frontino, Colombia. Basel 432a. Lectotype. Scale line equals 10 mm.

Form *chiriquiensis*—*Panama:* PANAMÁ—Cerro Campana (MCZ, CNHM 117647). CANAL ZONE—near Madden Lake (CNHM 56590). COCLÉ—El Valle (CNHM 63774, CNHM 63775, ANSP 226842); El Valle at 2,400 feet elevation (USNM 596736); trail to Las Minas (ANSP 163476); Club Campestre, El Valle (CNHM 73371, CNHM 73377, CNHM 73410, CNHM 73584, CNHM 84492). BOCAS DEL TORO—Chiriquí Lagoon (ANSP 5612 types of *chiriquiensis*).

Diagnosis.—The prominent, slightly sinuately twisted lamella does not reach the only slightly elevated parietal lip; parietal lip with outer edge slightly concave; basal lip with single knob-like tooth; lower palatal wall with or without an entering lamellar ridge, posteriorly with a hooked to "T"-shaped tooth (fig. 29a–f); periphery acutely carinated with protruding knife-edge keel; umbilicus only slightly obscured by extension of basal and parietal lips; spire normally elevated, rounded above; color yellow-white to light yellow-brown with spiral red sub- and supra-sutural color bands. Diameter 23.9–33.8 mm., H/D ratio 0.322–0.454.

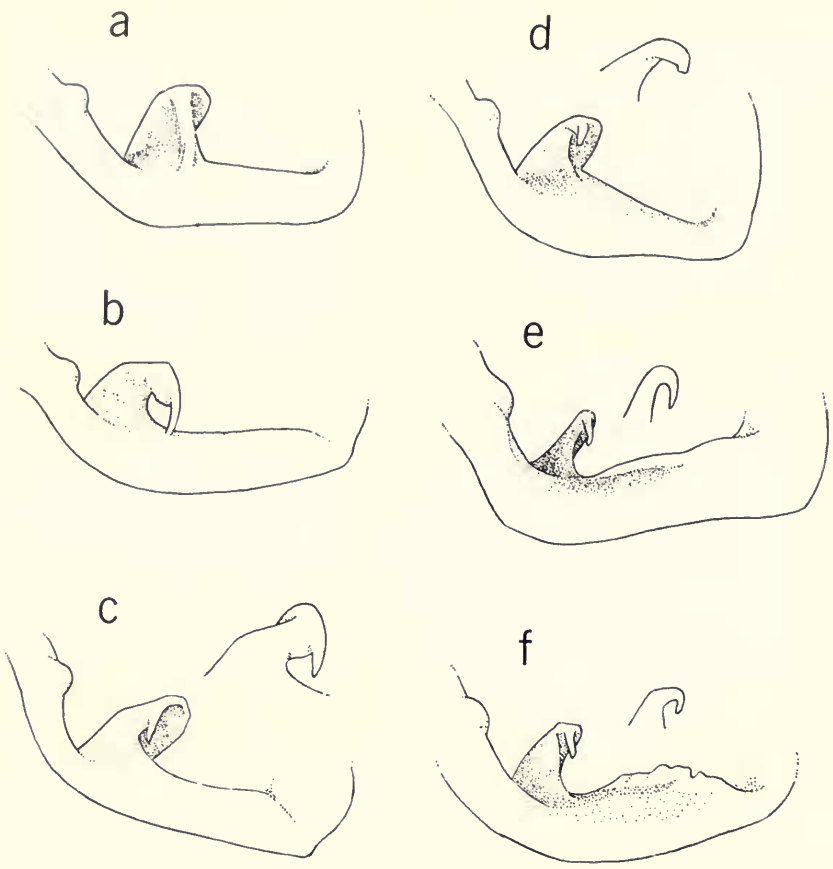


FIG. 29. Palatal tooth variation in *Labyrinthus unciger*; *a*, Form *tau*, Bocas del Toro Island, Panama, ANSP 140303. Lectotype of *tau* Pilsbry, 1926; *b*, Form *chiriquiensis*, on trail from El Valle to Río La Mina, Coclé Province, Panama, ANSP 162476; *c*, Form *chiriquiensis*, Chiriqui Lagoon, Panama, ANSP 5612. Lectotype of *chiriquiensis* Pilsbry, 1910; *d*, Form *chiriquiensis*, Club Campestre, El Valle, Coclé Province, Panama, CNHM 73371; *e–f*, Form *unciger*, Acandi, Chocó, Colombia, ANSP 164970, showing smooth (*e*) and fluted (*f*) ridge of lower palatal tooth.

Remarks.—Pilsbry (1926, p. 76) considered *unciger* and *chiriquiensis* distinct species and that *tau* was a mutant form of *chiriquiensis*. The differences were based on the structure and position of the palatal tooth. In typical *unciger* there is a lower palatal ridge arising just below the periphery that becomes markedly elevated with gradual posterior descension and slants diagonally backward. A large, slightly twisted, hook-like tooth, usually with a faint trace of an

outer lateral support, arises from the posterior edge of the lamella. The anterior edge of the ridge may be smooth (fig. 29e) or fluted (fig. 29f). The tip of the hook points downward (see fig. 29e, f). At Cerro Campana and El Valle, the anterior ridge has been reduced to a low callus and the hook-like tooth has developed very prominent outer and inner lateral projections and an extensive supporting buttress under the posterior two-thirds of the tooth (fig. 29d). The tooth still occupies the same relative position in the aperture. In the types of *chiriquiensis*, the tooth is located much nearer to the apertural edge, the inner lateral projection is very large, and the free portion is much shorter (fig. 29c). A few shells have the tooth joined to the base of the shell with only a slight ovate opening separating the tooth edge and buttress (fig. 29b). From this to form *tau* (fig. 29a) involves only closure of the opening separating the tooth edge and buttress. In the latter the tooth has turned into a "T"-shaped lamella with nearly vertical anterior descension.

The gradual shift in the tooth structure suggests classic clinal variation, but is complicated by both *tau* and *unciger* having been recorded from Acandi and both *unciger* and *chiriquiensis* at Cerro Campana. The collections, in both cases, were made at different times and could easily have been samplings of different local populations. Except for the Acandi, Colombia examples, all specimens from the Canal Zone south are *unciger*, which also reaches Cerro Campana, while those from the Canal Zone to Bocas del Toro are *chiriquiensis* and *tau*, except for the Cerro Campana *unciger*. The palatal tooth is located much farther back in the *unciger* form than in *chiriquiensis* and *tau*, and in every case tooth position follows tooth structure. Pending collections to determine the status of the Cerro Campana and Acandi mixture of forms, I prefer to treat these as nomenclaturally neutral "forms" rather than to recognize *unciger* and *chiriquiensis* as subspecies.

The striking color pattern of spiral reddish-brown bands on a yellowish-white background is diagnostic among Panama species and is only matched in *Labyrinthus* by *L. dunkeri* (Pfeiffer) from Santander, Magdalena and Goajira in Colombia. The latter is smaller with quite different dentition, the two basal and three palatal teeth at once separating them.

Size variation is moderately large between localities, but shows no obvious geographical trend. The vast majority of the specimens were between 28 and 31 mm. in diameter, with very few appreciably larger or smaller. The largest specimens were those from Arquía (CNHM

113998, CNHM 114110, 31.4–33.6 mm.) and Acandi (ANSP 164970, 31.3–33.8 mm.) in Chocó, Colombia and the Río Pucro, Darién, Panama (ANSP 140505, 33.4 mm.), yet the smallest specimen, probably a dwarf, was from the Golfo de Urabá (Barker, 23.9 mm.). Slightly smaller than average specimens were seen from Chiriquí Lagoon, Bocas del Toro Island, and Río Salud in Colon (see Table IX). A single specimen from Mona Creek, Almirante (ANSP 140304) was 30.8 mm. in diameter, so it is not possible to postulate a clinal variation in size from Colombia to Bocas del Toro. Few sets contained enough specimens to provide statistically significant data on variation, and most of those were from El Valle. These sets were collected in 1936, 1938, 1958 and 1959. With the possible exception of those taken by Fairchild in 1958, all came from the restricted patch of woodland behind the Club Campestre at the foot of the cliffs. The Fairchild collection might have come either from the cliff top areas or from the same population as the other materials. The differences in measurements (Table IX) are obviously insignificant, indeed almost unbelievably small. The length of life of *L. unciger* is unknown, but available collections cover at least two generations and indicate practically no variation in size, despite being from a habitat with extreme variations in annual rainfall patterns.

Comparison of samples from different geographic areas does, in some cases, show significant size differences. The "t" test difference between shells from Bocas del Toro Island (ANSP 104303) and El Valle specimens (CNHM 63775) is highly significant for diameter and H/D ratio ($n=18$, $t=3.550$ for diameter, $t=3.6103$ for H/D ratio), which is well below the 0.01 probability level. Other samples, such as *chiriquiensis* from Cerro Campana (MCZ) and Chiriquí Lagoon (ANSP 5612), do not differ significantly, having relatively high probabilities (0.20–0.50) of the variation being included in sampling error. More adequate collections are obviously needed before the extent and meaning of size variation can be judged.

Labyrinthus creveauxianus (Ancey, 1890). Figures 27c–d, 28.

Helix (*Labyrinthus*) *uncigera* var., Dohrn, 1875, Jahrb. deutsch. malacozool. Gesell., **2**, pp. 297–298—Frontino, Colombia (Wallis!); Pilsbry, 1889, Man. Conch. (2), **5**, p. 165.

Helix creveauxiana Ancey, 1890, Bull. Soc. Malac. France, **7**, p. 152—Frontino, Colombia (based on Dohrn, *loc. cit.*).

Caracolus (*Labyrinthus*) *uncigera* var. *creveauxiana* (Ancey), Pilsbry, 1892, Man. Conch. (2), **8**, p. 264.

TABLE IX.—Size and shape variation in *Labyrinthus unciger*

Species and set	No. of specimens	Height			Diameter			H/D ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
L. unciger										
MCZ 88932; 2,500 feet El Valle, Panama, 1938	13	11.9	10.9–13.0	0.18	30.0	28.3–31.2	0.25	0.397	0.354–0.444	0.007
CNHM 73410 and CNHM 73377; El Valle, Panama, 1959	5	11.5	11.0–11.8	0.13	30.1	28.6–32.4	0.64	0.383	0.339–0.402	0.011
CNHM 73371; El Valle, Panama, 1958	5	12.1	11.3–12.8	0.27	30.2	29.3–30.8	0.30	0.401	0.367–0.437	0.011
ANSP 226842 and CNHM 63774; El Valle, Panama, 1936	6	11.6	11.2–11.9	0.11	30.7	28.9–32.1	0.53	0.380	0.359–0.407	0.008
ANSP 63775; El Valle, Panama	16	11.9	10.3–13.5	0.18	30.6	28.1–32.8	0.27	0.389	0.336–0.429	0.006
USNM 341768; Acandi, Colombia	3	12.9	12.7–13.0	0.09	30.0	29.4–30.8	0.42	0.429	0.422–0.439	0.005
MCZ; Cerro Campana, Panama	11	12.2	11.1–12.9	0.16	30.4	29.3–32.0	0.24	0.400	0.366–0.425	0.005
MCZ; Cerro Campana, Panama	3	11.2	10.6–12.3	0.55	27.8	26.8–29.3	0.76	0.402	0.391–0.420	0.009
ANSP 155387; Río Salud, Panama	4	10.9	10.1–11.8	0.37	27.9	26.5–29.5	0.65	0.391	0.343–0.434	0.019
ANSP 5612; Chiriquí Lagoon, Panama	3	12.1	11.4–12.5	0.35	27.8	27.6–28.1	0.17	0.431	0.406–0.454	0.014
ANSP 104303; Bocas del Toro Island, Panama	4	12.4	12.1–12.7	0.14	28.7	28.4–29.1	0.05	0.432	0.421–0.440	0.005

Helix (Labyrinthus) uncigera frontinensis Kobelt, 1893, Syst. Conch. Cab., I (12), 4, p. 632, pl. 181, figs. 10–12 (plate issued in 1886).

Range.—The only definite locality is Frontino, Antioquia, Colombia.

Material.—*Colombia:* ANTIOQUIA—Frontino (Basel 432a—lectotype and paratype, Edinburgh, CNHM 132551, paratypes). No exact locality; ANSP 8915, MCZ, Zurich ("Colombia"); CM 62.13580 ("Panama"); CNHM 248 ("Ecuador").

Diagnosis.—The prominent, sinuately twisted parietal lamella stops just before or barely joins the elevated parietal lip; parietal lip straight or with outer edge convex; basal lip slightly sinuated with thick, very prominent, crescentic lamellar tooth; lower palatal wall with a diagonally entering lamella, posteriorly with a hooked tooth nearly touching the lamella, strong inner lateral buttress; periphery acutely angulated with protruding knife-edge keel; umbilicus only slightly obscured by basal and parietal lips; spire normally elevated, sides slightly rounded; color yellow-brown, lighter on keel, lip white, aperture darkly stained on palatal wall. Diameter 31.85–37.7 mm. (mean 35.5 mm.), H/D ratio 0.364–0.450 (mean 0.412).

Remarks.—The uniform brown color, union of the parietal lamella with the more strongly raised and straight or convex parietal lip, high basal lamella with the hooked tooth and slightly larger size are the main characters separating *creveauxianus* from the closely related *L. unciger* (Petit). The latter is common at low or medium elevations, while *creveauxianus* has been found only at the high country near Frontino. It may prove to be a montane derivative and could occur on the higher peaks of Darién in Panama, as seemingly does the bulimulid *Sultana (Clathorthalicus) wallisi* (Strebel). A single set in the Mousson collection labeled "Ocanna Wallis 1875" seems dubiously labeled.

Variation in the lower palatal tooth is less extensive than in *L. unciger*. Most examples of *L. creveauxianus* had a simple hook, although in one example the tip almost touched the palatal wall. Some specimens seen had the tooth with moderately developed lateral buttresses.

Group of *Labyrinthus otis*

The four species are characterized by having the lower palatal tooth developed into a high transverse lamellar plate or conical, slanted ridge; a single basal tooth; a sinuately twisted parietal lamella that meets the parietal lip; and a carinated periphery. The condition

of the lower palatal tooth is the simplest in *L. marmatensis*, with the tooth a high conical or spade-shaped ridge that is only moderately recessed (see fig. 36e). In *L. plicatus* the broader, higher ridge has the basic form found in *L. otis* and *L. subplanatus*, but is not as large. In the latter two species the aperture is literally choked with the huge teeth and the snail has to undergo real contortions in withdrawing and extending its body through the armature.

In contrast with species of the *isodon* and *aenigmus* groups, those of the *otis* complex have rather wide geographic ranges and show fairly extensive size variation. Two species, *L. otis* and *L. subplanatus*, are divided into subspecies and also have overlapping distributions. The ranges of *L. plicatus* and *L. marmatensis* seem to be isolated from the others. Possibly *L. euclausus* Beddome, 1908 (see p. 125) also belongs to this complex.

KEY TO THE LABYRINTHUS OTIS COMPLEX

1. Lower palatal tooth nearly touching parietal lamella; basal lip usually markedly sinuated 2
   Lower palatal tooth separated from parietal lamella by a wide gap; basal lip nearly straight or weakly sinuated 6
2. No deep supraperipheral sulcus on last one-quarter whorl 3
   Deep supraperipheral sulcus on last one-quarter whorl.
   Labyrinthus otis otis (Lightfoot, 1786)
3. Periphery without strongly developed apertural notch 4
   Periphery with strongly developed apertural notch or spout 5
4. Colombia; basal lip more strongly sinuated; basal and parietal lips dipping more into umbilicus ..... *Labyrinthus subplanatus subplanatus* (Petit, 1843)
   Costa Rica and Panama; basal lip less sinuated; basal and parietal lips dipping less into umbilicus ..... *Labyrinthus otis orthorhinus* Pilsbry, 1910
5. Apertural notch at periphery turned slightly to strongly upward.
   Labyrinthus subplanatus erectus (Mousson, 1873)
   Apertural notch at periphery reflected up to form a rounded spout.
   Labyrinthus subplanatus sipunculatus (Forbes, 1850)
6. Parietal lamella merging diagonally with parietal lip; Cauca River Valley.
   Labyrinthus marmatensis Pilsbry, 1910
   Parietal lamella merging almost perpendicularly with parietal lip; Venezuela.
   Labyrinthus plicatus (Born, 1780)

Differences between some of the forms recognized as subspecies of different species are rather subtle and difficult to present adequately in keys. Where species and subspecies could be confused, the non-overlapping geographic ranges (fig. 59) enable easy separation. For convenience, brief diagnoses of the species are presented here, as well as the more expanded diagnoses under each nomenclatural unit.

L. marmatensis Pilsbry, 1910—small shells (diameter 32 mm.) with nearly straight basal lip, small teeth, flat spire (mean H/D ratio 0.363) and the parietal lamella merging diagonally with the parietal lip (fig. 36e). Caldas and Antioquia in Colombia.

L. plicatus (Born, 1780)—much larger shells (diameter 36–53 mm.) with straight basal lip, small teeth, higher spire (H/D ratio 0.405–0.450), and parietal lamella meeting parietal lip perpendicularly. Aragua, Carabobo, Yaracuy and Falcón in Venezuela.

L. otis (Lightfoot, 1786)—large shells (diameter 34–58 mm.) with massive teeth choking the aperture, strongly sinuated parietal and basal lip and, in the Colombian subspecies, a very conspicuous, deep supraperipheral groove on the last one-quarter of the body whorl. Cundinamarca, Santander, Bolívar, Antioquia and Chocó in Colombia, north through Panama to Veraguas and Coclé, then as a probably relict population in the Golfo Dulce region of Costa Rica.

L. subplanatus (Petit, 1843)—smaller shells (diameter 34–45 mm.) with weak supraperipheral groove, very strongly sinuated basal lip, and in one subspecies, the peripheral notch reflected upward to form a spout. A disjunctive distribution in Colombia, with the nominate race extending from Norte de Santander to Cundinamarca in the Cordillera Oriental and one record from Caldas in the Cordillera Central; two subspecies ranging from Valle de Cauca north through Chocó and Darién as far as Cerro Campana, Panamá Province, Panama.

Considerable confusion existed in the older literature concerning the identity of the names proposed for these forms and their relationships. The original illustrations can be interpreted many ways and the original specimens of all but *L. plicatus* are doubtfully extant. It is thus far simpler to accept Deshayes (1838) clear separation of *L. plicatus* and *L. otis* than to worry about ancient citations. Dr. O. Paget has kindly informed me that the original specimens of *L. plicatus* (Born, 1780) are still preserved in Vienna and the species is correctly identified. *L. otis* and *L. subplanatus* have continually been confused, mostly because of lack of detailed locality records. *L. subplanatus* is very similar to the Panamanian *L. otis orthorhinus*, differing primarily by its more sinuated basal lip and less acutely carinated shell. *L. otis otis* differs strikingly from *L. subplanatus* in having the deep supraperipheral groove and in being much larger. The latter two have not been collected at the same locality and their ranges are only partly overlapping.

Labyrinthus otis (Lightfoot, 1786)

The specific name has normally been credited to Daniel Solander, but Dance (1962) has shown that the anonymous *Portland Catalogue* should be attributed to the Rev. John Lightfoot.

The species is easily divisible into two subspecies:

L. otis otis (Lightfoot, 1786)—last quarter of body whorl with a deep, narrow supraperipheral groove, parietal lip strongly sinuated, inner margin running parallel or nearly parallel with the inner margin of the basal lip. Rather widely distributed in Cundinamarca, Santander, Bolívar, Antioquia and Chocó.

L. otis orthorhinus Pilsbry, 1910—supraperipheral groove very faint or at most broad and shallow, parietal lip not as strongly sinuated and rarely parallel to the basal lip margin. Found from the Colombian–Panamanian border to El Valle, Coclé and the Azuero Peninsula region of Veraguas, then in San José, Costa Rica.

No obviously intermediate examples are known, but so little collecting has been done in Chocó and Darién that this is not surprising.

Labyrinthus otis otis (Lightfoot, 1786). Figures 30a–b, 31b.

Favanne, 1780, La Conchyliologie, pl. 63, fig. F 11.

Helix otis Lightfoot, 1786, A catalogue of the Portland Museum . . ., p. 38, lot No. 925 and p. 53, No. 1260 (based on Favanne, *loc. cit.*).

Helix labyrinthus Chemnitz, 1795, Syst. Conch. Cab., ed. 1, **11**, pp. 271–272, pl. 208, fig. 2048 (copied from Favanne)[1]; Deshayes, 1838, Guerin's Mag. de Zool., **1838**, pl. 111, fig. 1—Panama; Pfeiffer, 1847, Syst. Conch. Cab., 2nd ed., I (12), **1**, p. 61, pl. 2, fig. 5 (copy of figure in first edition); Deshayes, 1851, Hist. Nat. Moll., **1**, pp. 388–390, pl. 54B, fig. 5 (plate issued in 1823); Pfeiffer, 1852, Syst. Conch. Cab., I (12), **2**, p. 205; Reeve, 1852, Conch. Icon., *Helix*, pl. 100, fig. 550—Central America.

Helix (*Labyrinthus*) *labyrinthus* Deshayes, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 161–163 (partly), pl. 39, figs. 87–90.

Labyrinthus plicatus Martens, 1893 (not Born, 1780), Biol. Centr. Amer., Moll., p. 177.

Pleurodonte (*Labyrinthus*) *labyrinthus* (Deshayes), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95.

Pleurodonte (*Labyrinthus*) *otis* (Solander), Pilsbry, 1910, Proc. Acad. Nat. Sci., Philadelphia, **1910**, p. 504, pl. 37, figs. 5–7; Pilsbry, 1926, *op. cit.*, **78**, pp. 74–75—Cartagena (Lloyd B. Smith!).

Range.—Colombia: Cundinamarca, Santander, Bolívar, Antioquia, Chocó.

[1] Ruled a non-binomial work by Opinion 184 of the International Commission on Zoological Nomenclature.

Material.—Colombia: CUNDINAMARCA (Zurich)—Monteredondo at km. 76 on road from Bogotá to Villavicencio (CNHM 113995, CNHM 113996). SANTANDER—45 miles southeast of Barrancábermeja (USNM 341476). BOLIVAR—Quebrada Salvajín, Río Esmerelda, Upper Río Sinú (USNM 601776); Upper Río Uré, Río San Jorge (CNHM 133263); Limón, west of Montería, Río Sinú (USNM 364339); road between Río San Jorge and Palmavirál (ANSP 160144, MCZ 95722); La Burra (R. Wright Barker); La Unión (CNHM 117527); Río Canalete, ½ mile above La Unión (USNM 364338); near Cartagena (ANSP 111651, CM 62.39790). ANTIOQUIA—Turbo and León Valley to the south (USNM 543479, CNHM 71045); Gulf of Urabá (R. Wright Barker, Basel 5432a); Punta Piedras, near Nicolí, Gulf of Urabá (CNHM 113925). CHOCO —15 km. inland, Río Nuquí (USNM 488859); between Puerta Ardita and Coredó (CNHM 113888).

Diagnosis.—The high, sinuated parietal lamella merges diagonally with the parietal lip; basal lip slightly sinuated with single, thick, twisted lamella; lower palatal lip nearly straight with huge transverse, diagonal lamellar tooth nearly touching parietal lamella; periphery with narrow notch slightly reflected upward, last one-quarter of body whorl with deep supraperipheral sulcus; upper palatal lip with recessed crescentic lamella above upper edge of lower palatal tooth; parietal and basal lips usually run parallel into umbilicus; spire normally elevated, rounded above; color dark yellow brown. Diameter 39–54 mm., H/D ratio 0.400–0.483.

Remarks.—The very pronounced supraperipheral groove on the last one-quarter whorl and the tendency of the umbilical extension to narrow with the parietal and basal lips running parallel are the diagnostic characters. No specimens intergrading between *otis* and *orthorhinus* were seen, but probably will be collected eventually in southern Darién or the Atrato River basin.

Most of the specimens were between 45 and 54 mm. in diameter. In only a few cases were more than single shells seen from any one locality. Variability in these sets is covered in Table X. Sets from Chocó, Bolívar and Antioquia averaged 50.1, 47.7 and 47.4 mm. in diameter. These differences are significant at the 0.05 probability level when either of the smaller is compared with the larger, but the differences between the two smaller are not significant. A single specimen from Monteredondo is much smaller (diameter 41.6 mm.) and a dwarfed population from near Cartagena averaged 39.5 mm.

TABLE X.—Size and shape variation in *Labyrinthus o. otis* and *L. o. orthorhinus*

Species and set	No. of specimens	Height			Diameter			H/D ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
L. o. otis										
ANSP 111651; Cartagena, Colombia	3	18.0	17.8–18.2	0.12	39.5	39.3–39.7	0.12	0.455	0.452–0.458	0.002
USNM 543479; Turbo and Leon Valleys, Antioquia, Colombia	5	21.1	20.0–22.2	0.39	47.4	45.8–48.8	0.62	0.447	0.437–0.458	0.005
ANSP 160144; Palmaviral and San Jorge, Bolívar, Colombia	6	21.0	19.8–22.3	0.35	47.7	45.4–49.0	0.54	0.442	0.430–0.456	0.004
USNM 488859; Rio Nuquí, Chocó, Colombia	8	22.0	20.4–23.6	0.41	50.1	47.5–52.7	0.70	0.438	0.402–0.483	0.008
L. o. orthorhinus										
ANSP 101308; Tabernillo, Panama	13	18.4	17.3–23.2	0.43	41.7	39.5–44.5	0.38	0.441	0.407–0.574	0.012
CNHM; Barro Colorado Island, Panama, 1959	10	16.2	15.3–17.4	0.25	38.4	36.5–40.7	0.39	0.421	0.394–0.441	0.005
CNHM 63771; Barro Colorado Island, Panama	13	16.1	14.5–18.1	0.25	37.4	35.3–40.2	0.45	0.431	0.403–0.476	0.006
MCZ 111160; Barro Colorado Island, Panama, 1936	17	16.0	14.8–17.2	0.19	38.0	36.0–40.7	0.28	0.421	0.395–0.452	0.004
MCZ 85793; Barro Colorado Island, Panama, 1930	6	16.0	15.3–17.4	0.33	37.4	35.9–38.7	0.45	0.427	0.413–0.452	0.005

The single adult from the Upper Rio Uré (CNHM 133263) was collected on January 31, 1963. That evening it laid a cluster of eight whitish, globular eggs which, when preserved, measured 4.4–4.9 mm. in diameter. Unfortunately, the soft parts of the adult were not preserved.

Labyrinthus otis orthorhinus Pilsbry, 1910. Figures 30c–d, 31a.

Helix plicata Tate, 1866 (not Born, 1780), Amer. Jour. Conch., **5**, p. 156—north shore of Naval Bay, Colón, Panama.

Helix labyrinthus Deshayes, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 161–163 (partly), pl. 64, figs. 14–16 (from Gorgona, Canal Zone).

Pleurodonte (*Labyrinthus*) *labyrinthus* Pilsbry, 1894, *op. cit.*, **9**, pl. 25, figs. 4–5.

Pleurodonte (*Labyrinthus*) *plicata* Dall, 1909 (not Born, 1780), Smith. Misc. Coll., **52** (3), p. 361—Atrato River, "Sierra Darién" (A. E. Heighway!).

Pleurodonte (*Labyrinthus*) *otis orthorhinus* Pilsbry, 1910, Proc. Acad. Nat. Sci., Philadelphia, **1910**, pp. 502, 505, pl. 37, figs. 1–4—between Tabernillo and San Pablo, Canal Zone, Panama (Amos P. Brown!); Pilsbry, 1926, *op. cit.*, **78**, p. 75—near Gatún Dam, Canal Zone (A. A. Olsson!); near Darién and Alhajuela, Canal Zone (J. Zetek!); Quipo (=Cuipo), Colón (J. P. Chapin!); Upper Chagres (J. Zetek!); Pilsbry, 1930, *op. cit.*, **82**, p. 339—Barro Colorado Island, Canal Zone; hills near Mandingo River, head of Gulf of San Blas, Comarca de San Blas (Pilsbry!).

Pleurodonte labyrinthus Dall, 1912 (not Deshayes, 1838), Smith. Misc. Coll., **59** (18), p. 1, pl. 2, figs. 3–4—Santa Isabel, Colón (Pittier!).

Range.—Vicinity of Panamanian–Colombian border north to Golfo Dulce region of Costa Rica. Possibly absent from Chiriquí and Bocas del Toro, the Costa Rican populations being relicts.

Material.—Colombia: CHOCO—mountains near mouth of Atrato River (USNM 206288); Acandi (ANSP 150244). *Panama:* DARIÉN—Pintupo (ANSP 161811; Tacarcuna (MCZ 247232). COMARCA DE SAN BLAS—forest near Armila (USNM 228664); hills near Mandingo River, head of Gulf of San Blas (ANSP 151397, ANSP 243693). PANAMÁ—mountains around Gaspasalana, high Mamoní River (USNM 228907); between Chepo and Río Platanal (ANSP 162480); Río Indio, near Madden Lake (CNHM 20611); along ridge of Río Chico, fork of Río Pequení and Río Boquerón (ANSP 155410); La Aneida, near Tocumen Airport, 9 km. from Cerro Azul (CNHM 117035); slope of Cerro Cabra (ANSP 162486); hills above Arraiján (CNHM 125388); Cerro Trinidad (CNHM 117552, CNHM 132541); Cerro Campana (CNHM 73363, MCZ, USNM 596734). CANAL ZONE—between Tabernillo and San Pablo (ANSP 101306, ANSP 101308, CNHM 78829); near Empire (MCZ 45143); near Gorgona (MCZ 154015, ANSP 8907); Alhajuela

TABLE XI.—Size and shape variation in *Labyrinthus o. orthorhinus*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
L. o. orthorhinus													
ANSP 8907; Gorgona, Panama	4	17.7	15.5–19.4	0.81	42.4	39.7–43.9	0.93	0.417	0.363–0.449	0.020	12.8	11.8–14.4	0.56
MCZ 247232; Tacarcuna, Panama	4	16.6	16.3–16.9	0.12	40.9	40.1–41.7	0.41	0.406	0.398–0.420	0.005	10.3	9.5–10.9	0.29
ANSP 161811; Pintupo, Panama	8	19.7	18.8–21.5	0.30	49.8	48.5–53.1	0.54	0.395	0.375–0.422	0.005			
USNM 206288; near Atrato River mouth, Panama	11	18.4	15.7–19.7	0.35	43.3	38.7–44.9	0.54	0.425	0.406–0.445	0.004			
CNHM 132541 Cerro Trinidad, Panama	7	20.3	19.5–21.1	0.23	48.8	46.9–51.5	0.57	0.419	0.398–0.451	0.006	17.6	15.1–20.2	0.71
MCZ; Cerro Campana, Panama	4	20.0	16.7–21.8	1.15	50.4	43.9–54.5	2.27	0.397	0.381–0.413	0.007			
MCZ 88936; El Valle, Panama	4	21.0	19.0–22.6	0.74	53.2	48.7–55.6	1.53	0.395	0.390–0.407	0.004			
USNM 251424; Gatún, Panama	13	18.9	17.5–20.5	0.21	44.6	41.4–47.2	0.41	0.424	0.399–0.469	0.005			
MCZ 111166; Salamanca Hydrographic Station, Panama	11	19.0	17.7–20.8	0.24	47.8	45.3–50.5	0.46	0.398	0.350–0.424	0.006			
CNHM 117035; La Aneida, Tocumen, Panama	5	19.6	18.9–20.7	0.32	47.3	46.3–49.0	0.47	0.415	0.402–0.423	0.004			

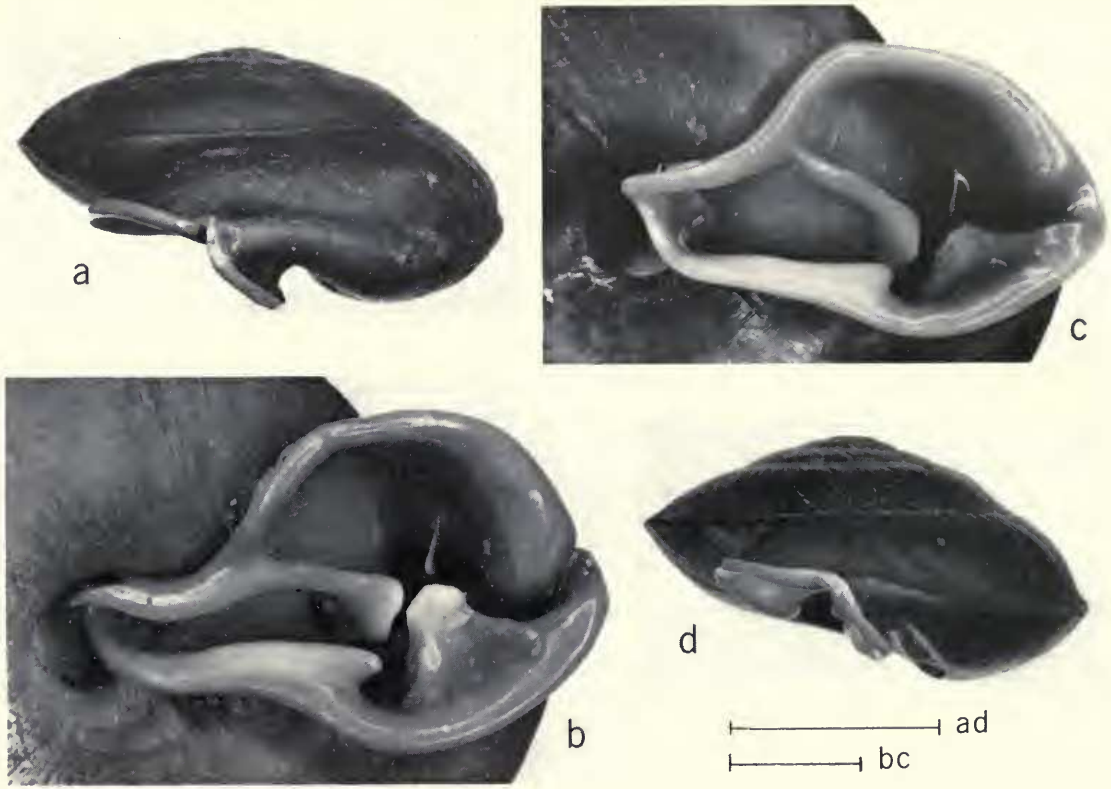


FIG. 30. Shells of: *a–b, Labyrinthus o. otis*, between Palmaviral and San Jorge, Bolívar, Colombia, ANSP 160144 (*a*, aperture; *b*, side); *c–d, Labyrinthus o. orthorhinus*, Arraijan, Panama, CNHM 125388 (*c*, aperture; *d*, side). Scale lines equal 10 mm.

(USNM 228665, USNM 251432, ANSP 162478); Gatún (USNM 251424, USNM 360669); Barro Colorado Island (numerous sets); Salamanca Hydrographic Station, Río Pequení (MCZ 111166, Jackson 4828); shore of Madden Lake (CNHM 73365, CNHM 73431,

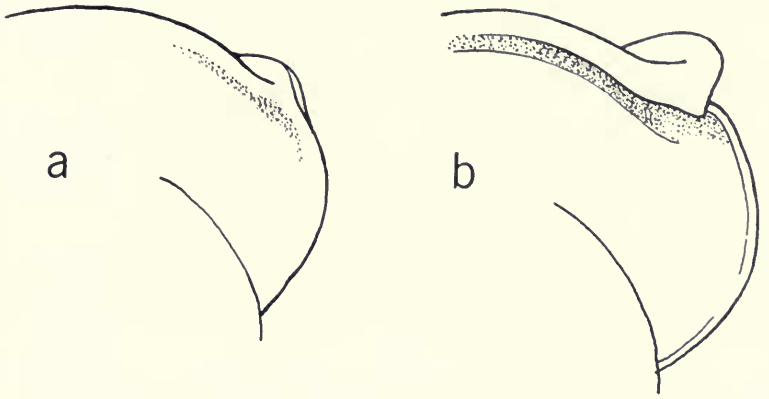


FIG. 31. Supraperipheral grooves in: *a*, *Labyrinthus o. orthorhinus*; *b*, *Labyrinthus o. otis*.

CNHM 84465, CNHM 125379, USNM 589728). COLON—Santa Isabel (USNM 228663); Quebrada Querquera, 15 miles NE of Colón (USNM 601014); near Cuipo (CNHM 63772, CNHM 63773); San Juanito, near Pegero, Coclé del Norte (USNM 618835). COCLÉ—El Valle (CNHM 63770, CNHM 73372, MCZ 88936, USNM 596735, ANSP 226920). VERAGUAS—(all in Azuero Peninsula area, collected by E. R. Dunn in 1940) Tres Punta (ANSP 184697); Avacada Camp at 2,100 feet elevation (ANSP 184696); Mangillo (ANSP 184698). *Costa Rica:* SAN JOSÉ—Santa María de Dota at 1,500 meters elevation (USNM 363817).

Diagnosis.—The high, sinuately twisted parietal lamella usually merges perpendicularly with the parietal lip; basal lip slightly sinuated with single thick, crescentic lamella; lower palatal lip with high, diagonally spade-shaped lamellar tooth nearly touching parietal lamella; periphery with faint internal groove, but no notch and only a faint supraperipheral sulcus on body whorl; upper palatal lip with a small to medium sized, crescentic lamella, recessed and above lower palatal tooth; parietal and basal lips usually not running parallel and only weakly dipping into umbilicus; spire normally elevated, sides flat or rounded above; color dark reddish or yellow brown. Diameter 34–58.5 mm., H/D ratio 0.350–0.476.

Remarks.—The usually perpendicular insertion of the parietal lamella on the parietal lip, lack of a supraperipheral sulcus and less deep penetration of the basal and parietal lips into the umbilicus easily separate *L. o. orthorhinus* from the nominate subspecies. Adequate collections may show that these are non-intergrading allopatric populations, but variability in the observed material suggests that they will be shown to be subspecially related morphs.

Comparatively simple variation is shown in most populations of this species. Shells from wetter areas are significantly larger than those from drier zones, areas such as Cerro Cabra near the Pacific Coast having dwarfed specimens (diameter 39.1–39.6 mm.) while those from Gatún (mean diameter 44.6 mm.) or Armita (mean diameter 44.5 mm.) are significantly larger. Size variation in a number of populations is summarized in Tables X and XI.

The few examples known from Cerro Campana, El Valle and Coclé del Norte, are, with three exceptions, extremely large, ranging from 48.7–58.5 mm. in diameter. James Zetek had two shells labeled "El Valle" that are only 36.6–37.1 mm. in diameter, while one specimen from Cerro Campana was only 43.9 mm. in diameter. The Zetek shells might have been mislabeled. The specimens from Cerro Trinidad (CNHM 132541) are somewhat smaller (mean diameter 48.8 mm.), but well above the size of most Canal Zone populations. Samples from Pintupo, Darién (mean diameter 49.8 mm.), La Aneida near Cerro Azul (47.3 mm.), Salamanca Hydrographic Station (47.8 mm.), and Gatún (44.6 mm.) are also rather large. Material from Tacarcuna, Darién (40.9 mm.), Gorgona, Canal Zone (42.4 mm.) and the types from between Tabernillo and San Pablo (41.6 mm.) are distinctly smaller.

Apparently the Barro Colorado Island population is dwarfed. Dated sets from 1930, 1936 and 1959 plus several undated series all showed mean diameters of 37.4–38.4 mm. No collections from adjacent mainland areas have been made and it is unknown if the Barro Colorado Island specimens are exceptionally dwarfed or merely representative of equally dwarfed populations in the general region. "Small island" dwarfed populations of land snail species are known, but the situation of the Barro Colorado Island shells remains to be investigated. It is known that Barro Colorado has an exceedingly heavy population of coatis. These occasionally eat *L. otis orthorhinus* (Kaufmann, 1962, p. 183). The coati has a very difficult time cracking the shell and usually depends on other food sources (personal communication from Dr. Kaufmann). Despite this, the possibility

must be considered that the coatis provide a selective pressure for smaller size, since individuals less able to retreat into narrow crevices are more apt to be eaten. Even casual observation of foraging coatis brings forth great admiration for the thoroughness of their inspection of forest floor niches.

Most living specimens of *L. otis orthorhinus* have been taken near or under large fallen logs in at least moderately heavy forest. They aestivate in cracks in old logs and under logs and starting bark on the ground. During the very dry January of 1959 on Barro Colorado Island no living specimens were obtained. The wetter areas near Madden Lake in February of the same year yielded live specimens under hanging sheets of bark on old stumps at 5–7 feet above ground level. The strong development of the parietal and lower palatal teeth results in their nearly touching. Retraction and extension of the animal does not seem to be slowed by the large armature, but it does force the animal to retract and extend solely through the narrow passage between the parietal wall and basal lip. Observation of the exact process was difficult, but it appears that expansion is virtually complete before the thin roof of the pallial cavity is extended through the gap between the parietal and lower palatal lamellae. The muscular mantle collar has been extended past this point and thus does not have to squeeze between. The collar and pallial wall is then appressed to the upper and outer lip edges. The reverse process occurs on retraction.

Labyrinthus subplanatus (Petit, 1843)

This smaller relative of *L. otis* is divided into three subspecies, one of which ranges into Central Panama. An isolated subspecies, *L. s. subplanatus*, is exceedingly similar to some specimens of the Panamanian *L. otis orthorhinus*. Conceivably, *subplanatus, s.s.*, could be a direct offshoot of typical *otis*, but the two have been found in the same region. For this reason and the presence of near intergrades I have chosen to associate it with the Western Colombian and Panamanian populations. No form of *subplanatus* has been dissected and only the *orthorhinus* form of *otis* is known anatomically.

The three subspecies of *L. subplanatus* can be separated as follows:

L. subplanatus subplanatus (Petit, 1843)—color light brown to speckled, basal lip moderately sinuated, peripheral notch a slight groove not twisted upward, size 34–45 mm. Caldas and Cundinamarca to Norte de Santander.

L. subplanatus erectus (Mousson, 1873)—color brown or speckled brown, basal lip sharply sinuated, peripheral notch slightly twisted

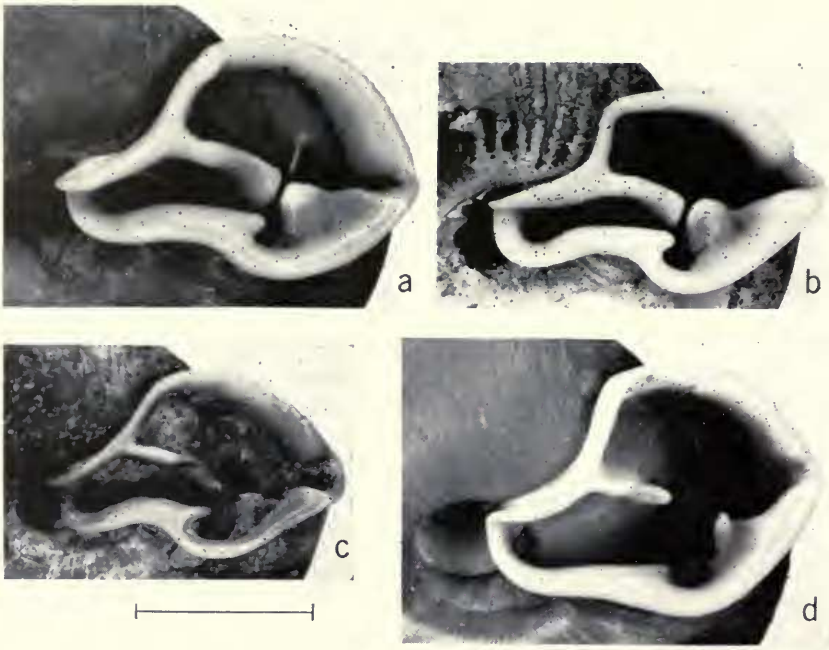


FIG. 32. Apertures in: *a*, *Labyrinthus s. subplanatus*, San Juan de Dios and San Juan del Silencio, Santander, Colombia. R. Wright Barker; *b*, *Labyrinthus s. erectus*, between Buenaventura and Río Calima, Valle de Cauca, Colombia, CNHM 113999; *c*, *Labyrinthus s. erectus*, Bogotá, Colombia. Zurich. Holotype; *d*, *Labyrinthus plicatus*, normal form, "Venezuela." Zurich. Scale line equals 10 mm.

upward, size 31–38 mm. Valle de Cauca, Antioquia, and Chocó, possibly Cundinamarca.

L. subplanatus sipunculatus (Forbes, 1850)—color light brown to reddish brown with yellow-white periphery, basal lip sharply sinuated, peripheral notch twisted sharply upward to form a spout, size 34–42 mm. Central Chocó to Panamá Province, Panama.

Labyrinthus subplanatus subplanatus (Petit, 1843). Figures 32a, 33a.

Carocolla subplanata Petit, 1843, Rev. Zool., **1843**, p. 238—New Granada (=Colombia); Petit, 1843, Guerin's Mag. de Zool., **1843**, pl. 68.

Helix labyrinthus var. Pfeiffer, 1848, Monog. helic. viv., **1**, p. 398; Pfeiffer, 1852, Syst. Conch. Cab., I (12), **2**, pp. 205–206, pl. 104, figs. 5–7 (plate issued in 1850).

Helix (*Labyrinthus*) *subplanatus* (Petit), Dohrn, 1875, Jahrb. deutsch. malac. Gesell., **2**, pp. 296–297.

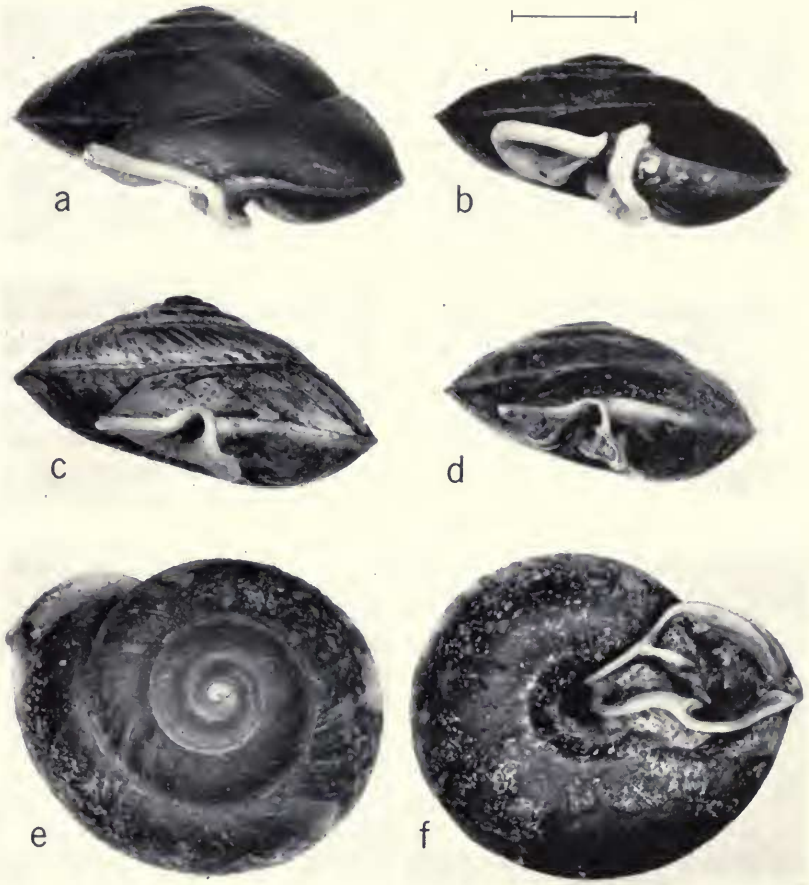


FIG. 33. Shells of: *a*, *Labyrinthus s. subplanatus*, San Juan de Dios and San Juan del Silencio, Santander, Colombia. R. Wright Barker; *b*, *Labyrinthus s. sipunculatus*, Finca "La Victoria," Río Baudó, Colombia, CNHM 113994; *c*, *Labyrinthus s. erectus*, between Buenaventura and Río Calima, Valle de Cauca, Colombia, CNHM 113999; *d–f*, *Labyrinthus s. erectus*, Bogotá, Colombia. Zurich. Holotype (*d*, side; *e*, top; *f*, base). Scale line equals 10 mm.

Helix (*Labyrinthus*) *labyrinthus* Deshayes, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 161–163, pl. 40, figs. 100–102 (partly).

Pleurodonte (*Labyrinthus*) *otis subplanatus* (Petit), Pilsbry, 1910, Proc. Acad. Nat. Sci., Philadelphia, **1910**, p. 504.

Range.—Cordillera Oriental of Colombia in Santander and Cundinamarca; Cordillera Central in Caldas. Possibly Sierra de Perijá in Norte de Santander.

Material.—Colombia: NORTE DE SANTANDER—Ocana (Zurich); Mt. Alto de la Cruz, Ocana (Zurich); dense jungle, 13 km. south of Puerto Santos (USNM 380794). SANTANDER—near Río Sucio at 600–800 feet elevation (USNM 363924); Río Lebrija valley at 1,000 feet elevation (USNM 601777); Rios San Juan de Dios and San Juan del Silencio, Carere (R. Wright Barker); south part of Santander (USNM 472800, CNHM 71044); Landázuri at 830 meters elevation (MCZ 179595). CALDAS—Victoria at 820 meters elevation (CNHM 113997).

Diagnosis.—The very prominent, sinuately twisted parietal lamella runs almost perpendicularly into the raised parietal lip; basal lip moderately to strongly sinuated, with very thick slanted lamella; periphery acutely angulated with protruding keel, small groove inside aperture, no deep supraperipheral sulcus; upper palatal lip with low, deeply recessed crescentic lamella located above apex of lower palatal tooth; basal and parietal lips dipping moderately deeply into umbilicus; spire generally strongly elevated, rounded above; color dark brown to speckled with greenish-yellow. Diameter 34.6–44.6 mm. (mean 38.3 mm.), H/D ratio 0.384–0.502 (mean 0.440).

Remarks.—The absence of a strong supraperipheral sulcus and the more nearly perpendicular insertion of the parietal lamella into the parietal lip are the main characters separating *subplanatus* from *otis otis*. *L. otis orthorhinus* is less readily distinguished, the differences from *subplanatus* of less sinuated basal lip and shallow dipping of the basal and parietal lips into the umbilicus being of degree. The ranges of *subplanatus* and *otis orthorhinus* are widely separated, so that there is little chance of confusion. Both *L. otis otis* and *L. subplanatus* have been reported from the same general areas, but not from the same locality.

Most specimens of *L. subplanatus* were 36–40 mm. in diameter. The single shell from Caldas was 41.5 mm. and the Landázuri example 44.6 mm. The diameter of the type was given as 40 mm. and the dark brown shell is matched by several specimens from Santander. Several examples were the greenish-speckled brown of *L. s. erectus*, but differ very slightly in having a less sinuated lip and no real reflection of the peripheral notch.

Labyrinthus subplanatus erectus (Mousson, 1873). Figures 32b–c, 33c–f.

Helix erecta Mousson, 1873, Malak. Blätt., **21**, pp. 3–4—Bogotá, Colombia (Wallis!); Pfeiffer, 1876, Novit. Conch., **4**, pp. 116–117, pl. 127, figs. 1–3;

Pfeiffer, 1876, Monog. helic. viv., **7**, p. 461; Pilsbry, 1889, Man. Conch. (2), **5**, p. 162, pl. 40, figs. 100–102.

Pleurodonte (*Labyrinthus*) *otis erecta* (Mousson), Pilsbry, 1910, Proc. Acad. Nat. Sci., Philadelphia, **1910**, p. 505.

Range.—Chocó and Valle de Cauca in Western Colombia, possibly Cundinamarca.

Material.—Colombia: CUNDINAMARCA—Bogotá (Zurich, types). VALLE DE CAUCA—region between Buenaventura and Río Calima (CNHM 113999, CNHM 117525); Anchicaya, between Cali and Buenaventura at 300–500 meters (SMF 162665); La Brea Calima, Municipio Buenaventura (MCZ 177962). CHOCO—Río Atrato (R. Wright Barker, CNHM 117526); 15 km. inland, Río Nuquí (USNM 488860). ANTIOQUIA—Frontino (Zurich). *"Ecuador"* (CNHM 40774).

Diagnosis.—The very high, sinuately twisted parietal lamella slants diagonally into the elevated parietal lip; basal lip strongly sinuated, with thick, slanted lamella; lower palatal lip nearly straight with very high transverse lamella; periphery acutely angulated with protruding knife-edge keel, peripheral notch distinctly reflected upward, no prominent supraperipheral sulcus; upper palatal lip with small crescentic lamella, deeply recessed, placed above apex of lower palatal tooth; basal and parietal lips dipping deeply into umbilicus; spire moderately elevated, sides flat or rounded above; color brownish, speckled with greenish-yellow flecks. Diameter 31.2–38.1 mm. (mean 34.2 mm.), H/D ratio 0.400–0.450 (mean 0.423).

Remarks.—The more sinuated basal lip, more angulated junction of the parietal lamella and lip, greater reflection upward of the peripheral notch and usually smaller size separate typical examples of *L. s. erectus* from *L. s. subplanatus*. Too little material is available to allow delineation of ranges or to show intergradation. The original locality of "Bogotá" is obviously of little meaning. Neither of the two specimens in the Mousson collection matches Pfeiffer's illustration (*loc. cit.*) or the dimensions given in the original description. The present locality of the Pfeiffer collection is unknown. Since Mousson could have been presumed to retain possession of good examples, I have chosen as lectotype the better preserved of the two cotypes (fig. 33d–f). The specimen is 31.2 mm. in diameter, 13.0 mm. high with slightly more than $4\frac{3}{4}$ whorls. The material from Chocó and Valle de Cauca is distinctly larger than the types, but the single shell from Frontino is also small. Further collecting may show that

TABLE XII.—Size and shape variation in *Labyrinthus s. subplanatus*, *L. s. sipunculatus* and *L. plicatus*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
L. s. subplanatus													
USNM 472800; Santander, Colombia	4	16.6	15.5–17.1	0.37	38.6	37.5–39.4	0.40	0.430	0.402–0.456	0.012			
L. s. sipunculatus													
USNM 622080; Pirri Range, Panama	4	16.1	15.0–17.4	0.53	41.0	38.7–42.4	0.87	0.389	0.360–0.424	0.014			
USNM 596996; Nuquí, Chocó, Colombia	4	15.8	15.0–16.4	0.31	36.0	34.6–37.9	0.71	0.441	0.396–0.464	0.015			
L. plicatus													
USNM 508782; El Mene, Venezuela	5	16.6	15.8–17.7	0.37	38.5	36.0–41.3	0.94	0.431	0.405–0.448	0.007			
MCZ 154932; Pauji, Venezuela	19	17.4	15.1–18.6	0.22	40.5	36.8–43.7	0.46	0.429	0.397–0.460	0.004	12.4	9.4–18.3	0.46
MCZ 63047; Palma Sola, Venezuela	27	17.3	15.8–18.6	0.14	40.9	38.2–42.9	0.24	0.424	0.397–0.462	0.004	11.9	10.0–15.7	0.30
ANSP 138643; Palma Sola, Venezuela	5	18.1	17.1–19.2	0.42	41.7	38.0–45.5	1.40	0.436	0.376–0.460	0.015	12.0	10.8–13.9	0.51
SMF 181617; Rancho Grande, Venezuela	9	17.5	16.6–19.0	0.22	37.6	36.2–38.9	0.26	0.465	0.449–0.502	0.006	12.2	10.6–14.5	0.39

the type locality is an error and that *erectus* is found only in the Atrato, San Juan and Calima river basins.

Intergradation between *erectus* and *sipunculatus* is present in a set collected in February, 1951 in a forest near Nuquí, Dept. Chocó (USNM 596996). The four specimens range from the typical spout of *sipunculatus* to a notch only slightly more developed than in typical *erectus* (see fig. 35).

Labyrinthus subplanatus sipunculatus (Forbes, 1850). Figures 33b, 34a, 35.

Helix labyrinthus var. *sipunculatus* Forbes, 1850, Proc. Zool. Soc. London, **1850**, p. 53, pl. 9, figs. 4a, b—Panama.

Helix annulifera Pfeiffer, 1852, Conch. Icon., *Helix*, pl. 100, fig. 555—Central America; Pfeiffer, 1853, Proc. Zool. Soc. London, **1851**, p. 260—Panama; Pfeiffer, 1853, Monog. helic. viv., **3**, p. 255.

Helix (*Labyrinthus*) *labyrinthus* var. *annulifera* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 162, pl. 42, figs. 32–33.

Labyrinthus annuliferus (Pfeiffer), Martens, 1893, Biol. Centr. Amer., Moll., p. 177.

Pleurodonte (*Labyrinthus*) *otis sipunculata* (Forbes), Pilsbry, 1910, Proc. Acad. Nat. Sci., Philadelphia, **1910**, p. 504.

Pleurodonte (*Labyrinthus*) *otis annulifera* (Pfeiffer), Pilsbry, 1910, *op. cit.*, **1910**, pp. 504–505.

Pleurodonte (*Labyrinthus*) *goldmani* Dall, 1912, Smith. Misc. Coll., **59** (18), pp. 1–2, pl. 2, figs. 1–2—Pirri Range, Darién, Panama (E. A. Goldman!).

Pleurodonte (*Labyrinthus*) *sipunculata* (Forbes), Pilsbry, 1926, Proc. Acad. Nat. Sci., Philadelphia, **78**, p. 74, pl. 9, fig. 4—Paya and Rio Tucuti. Darién, Panama (A. A. Olsson!).

Pleurodonte (*Labyrinthus*) *sipunculata annulifera* (Pfeiffer), Pilsbry, 1926, *op. cit.*, **78**, p. 74.

Range.—Rio Baudo and Nuquí, Chocó, Colombia north to Cerro Campana, Panamá Prov., Panama.

Material.—Colombia: CHOCO—Finca La Victoria, boca del Pepe, Río Baudo (CNHM 113994); Nuquí in forest (USNM 596996); mountains near mouth of Atrato River (USNM 206289). *Panama:* DARIÉN—Pirri Range (USNM 214403, USNM 622080 types of *goldmani*); Paya (ANSP 140306); Rio Tucuti (ANSP 140307). PANAMÁ—Cerro Campana (MCZ); Serra Chucanti at 1,800 feet elevation (USNM 620477). "*Ecuador*" (Zurich).

Diagnosis.—The high, sinuately twisted parietal lamella merges diagonally with the raised parietal lip; basal lip very strongly sinuated with thick, twisted lamellar tooth; lower palatal lip nearly

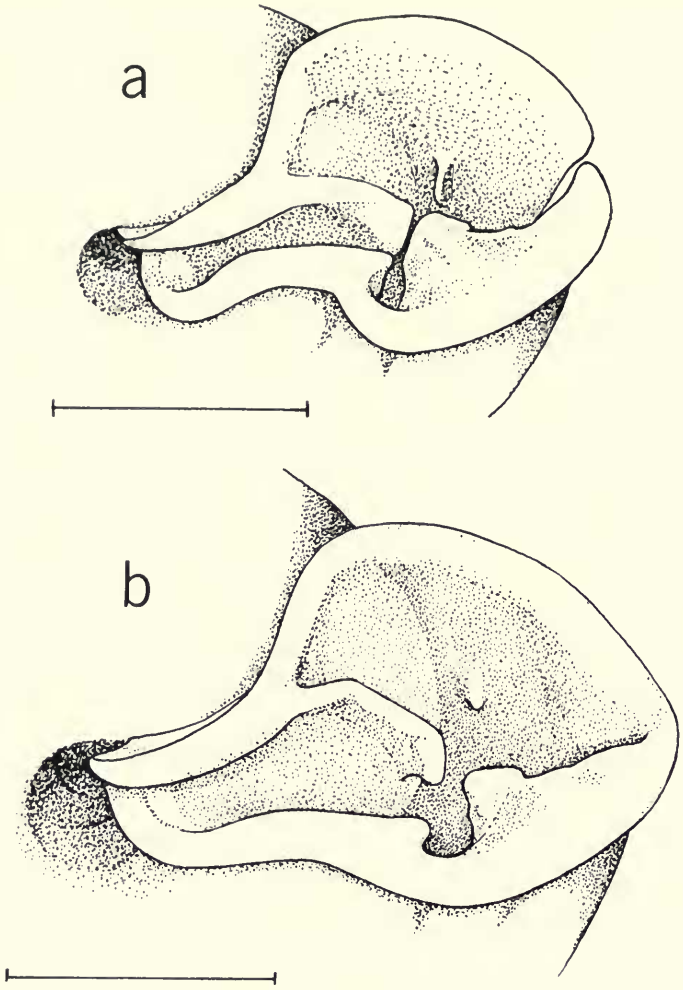


FIG. 34. Apertures of: *a*, *Labyrinthus s. sipunculatus*, Finca "La Victoria," Río Baudó, Colombia, CNHM 113994; *b*, *Labyrinthus plicatus*, heavy form, "Venezuela." Zurich. Scale lines equal 10 mm.

straight with very high transverse lamella; periphery acutely angulated with somewhat protruding keel, periphery with notch turned upward, connected by narrow groove to rest of aperture, no marked supraperipheral sulcus; upper palatal lip with low, deeply recessed crescentic lamella located above apex of lower palatal tooth; basal and parietal lips extending into umbilicus; spire strongly elevated, sides flat; color dark yellow brown to reddish brown with lighter pe-

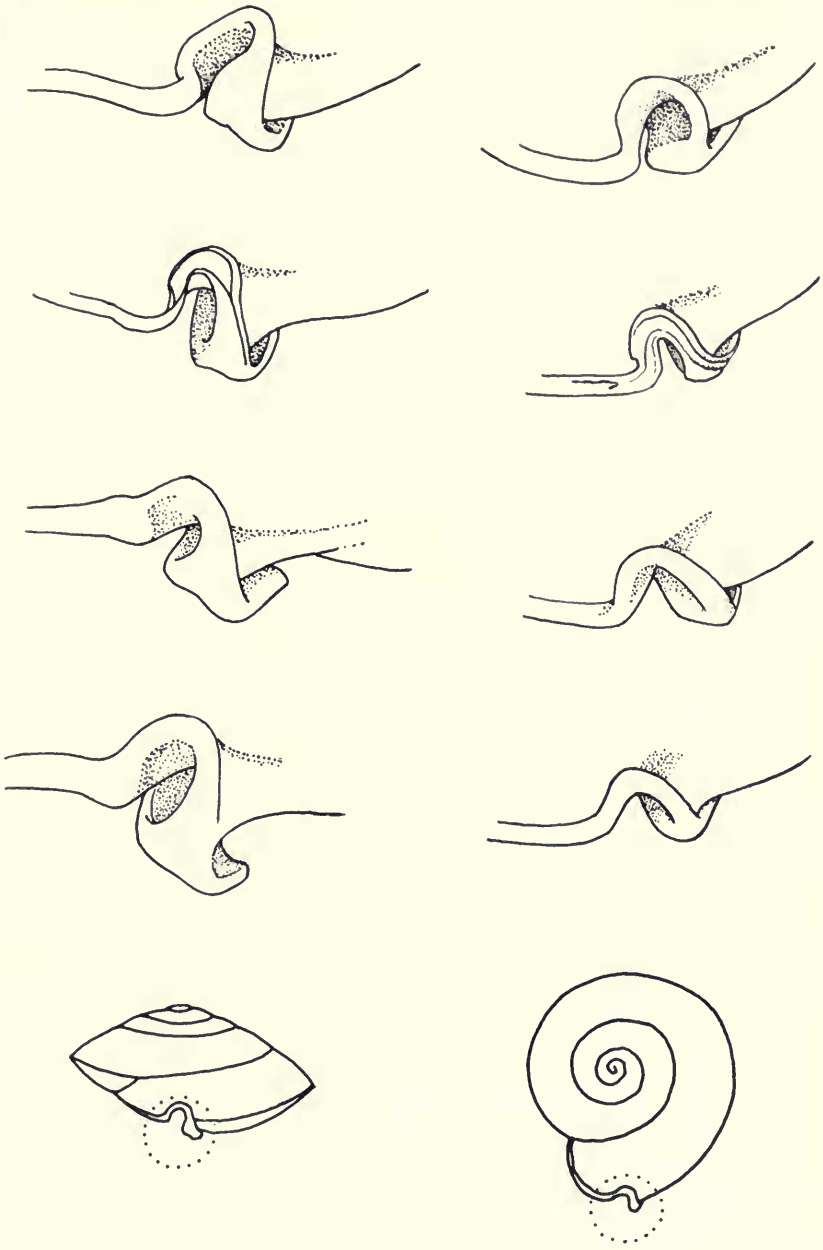


FIG. 35. Variation of peripheral notch in: *Labyrinthus s. sipunculatus*, Río Nuquí, Chocó, Colombia, USNM 596996.

ripheral zone. Diameter 33.9–42.4 mm. (mean 37.4 mm.), H/D ratio 0.360–0.464 (mean 0.411).

Remarks.—The extreme sinuosity of the basal lip and the upward reflection of the peripheral notch to form a spout are the main identifying characters. The specimens from Nuquí (see fig. 35) intergrade with *erectus*, and color variation connects the pale brown *sipunculatus* and the reddish-brown zoned *annuliferus*. The specimens on which *goldmani* Dall, 1912 was based are simply larger individuals of *sipunculatus*. Variation in two sets is summarized in Table XII. The record from Cerro Campana is rather surprising. Despite the very considerable collecting in the vicinity of the Canal Zone, no specimens of *sipunculatus* have been found between Cerro Campana and the Rio Tucuti. The specimens could have been mislabeled, but it is equally probable that the Cerro Campana shells came from a relict population.

Labyrinthus plicatus (Born, 1780). Figures 32d, 34b, 36a.

Helix plicata Born, 1780, Test. Musei Caesarei Vindobonensis, p. 368—East Indies (error). Based on Knorr, 1771, Vergnugen der Augen und des Gemüths, pt. V, pl. 26, fig. 5; Deshayes, 1838, Guerin's Mag. de Zool., pl. 110; Deshayes, 1851, Hist. Nat. Moll., **1**, pp. 387–388, pl. 54B, fig. 4; Pfeiffer, 1852, Syst. Conch. Cab., I (12), **2**, pp. 204–205, pl. 104, figs. 1–4 (plate issued in 1850); Reeve, 1852, Conch. Icon., *Helix*, pl. 100, figs. 553a–b.

Helix labyrinthus Lamarck, 1792, Jour. d'Hist. Nat., **2**, p. 352, pl. 42, fig. 4.

Carocolla hydiana Lea, 1838, Obs. Genus Unio, **2**, p. 98, pl. 23, fig. 73—near Puerto Cabello, Venezuela.

Helix (Labyrinthus) plicatus (Born), von Martens, 1873, Ges. Naturf. Fr. Berlin, Festschr., **1873**, p. 168—Puerto Cabello, Chino, Caracas, Venezuela; Pilsbry, 1889, Man. Conch. (2), **5**, pp. 163–164, pl. 63, figs. 1–5, 9.

Pleurodonte (Labyrinthus) plicata (Born), Pilsbry, 1894, Man. Conch. (2), **9**, p. 95; H. B. Baker, 1926, Occ. Pap. Univ. Michigan Mus. Zool., **167**, pp. 16–19, pl. 12, figs. 65–67, pl. 14, fig. 73—San Esteban Valley below Los Quiguas, Carabobo; Banco Largo near Bejuma, Carabobo; Palma Sola, Yaracuy; Quebrada Sucremo, Boquerón, Yaracuy.

Labyrinthus plicatus (Born), Wurtz, 1955, Proc. Acad. Nat. Sci., Philadelphia, **108**, pp. 113–117; Thompson, 1957, Occ. Pap. Univ. Michigan Mus. Zool., **591**, p. 5—Rancho Grande, Aragua, Falcón, Venezuela.

Range.—*Venezuela:* Aragua, Carabobo, Yaracuy, Falcón.

Material.—*Venezuela:* FALCON—El Mene and Riecito, Acosta (CNHM 71043, USNM 508782, USNM 499989, MCZ 64951); Tocuyo Valley, between Guaidima and Taparito (MCZ 115523); Pauji, Acosta (MCZ 154932). CARABOBO—Puerto Cabello (CM 62.-

12727); near Puerto Cabello (USNM 106002, ANSP 8910, ANSP 8912, types of *hydiana* Lea, MCZ 88156, MCZ 154016); 6 miles west of Puerto Cabello (USNM 214443); Chorim, Puerto Cabello (ANSP 8911); La Guaira (USNM 307393); Manuare (MCZ 172026). DISTRICTO FEDERALES—Catuche, Caracas (USNM 252689). YARACUY—Palma Sola (ANSP 138643, MCZ 63047). ARAGUA—Rancho Grande (MCZ 210889, SMF 181617).

Diagnosis.—The high, sinuated parietal lamella usually merges perpendicularly with the parietal lip; basal lip straight with a single thick, diagonally slanted tooth; lower palatal lip with large spade-shaped, diagonal lamella whose upper edge is well separated from the parietal lamella; periphery with internal groove, but no notch or supraperipheral sulcus; upper palatal wall with or without trace of a recessed, crescentic lamella above top edge of lower palatal tooth; parietal and basal lips only slightly dipping into umbilicus; spire normally elevated, rounded above; color yellow brown. Diameter 36–53 mm., H/D ratio 0.376–0.505.

Remarks.—Typical specimens show a greatly reduced dentition from that seen in *subplanatus* or *otis orthorhinus*. The lower palatal tooth is only a fraction of the size found in the preceding forms and there is a large spatial gap between the parietal and lower palatal lamellae. *L. otis otis* immediately differs in having the very strong supraperipheral sulcus on the last one-quarter whorl. The much smaller *L. marmatensis* differs in having the parietal lamella diagonally merging with the parietal lip, while in *plicatus* the parietal lamella inserts almost perpendicularly into the parietal lip (see figs. 34b, 36e).

The types of *Carocolla hydiana* Lea, 1838 (USNM 106002) are very large (diameter 50–53 mm.) individuals of *plicatus*, probably representative of populations from favorable moisture conditions. The vast majority of specimens are 38–43 mm. in diameter, with the extremes ranging from 36–45.5 mm. There have been no collections of individuals equaling the size of *hydiana* in the last 125 years. Size variation in five populations is summarized in Table XII.

Some specimens (MCZ 64951 from Cerro Riecito, Acosta and MCZ 115523 from Tocuyo Valley) have the lips greatly thickened (fig. 34b) and the apertural structure begins to approach *L. otis orthorhinus*. The upper palatal lip region is much less obstructed by the teeth and the lower palatal tooth is not as wide and is more spade-shaped than in *orthorhinus*. Possibly these are from drier areas than the typical forms.

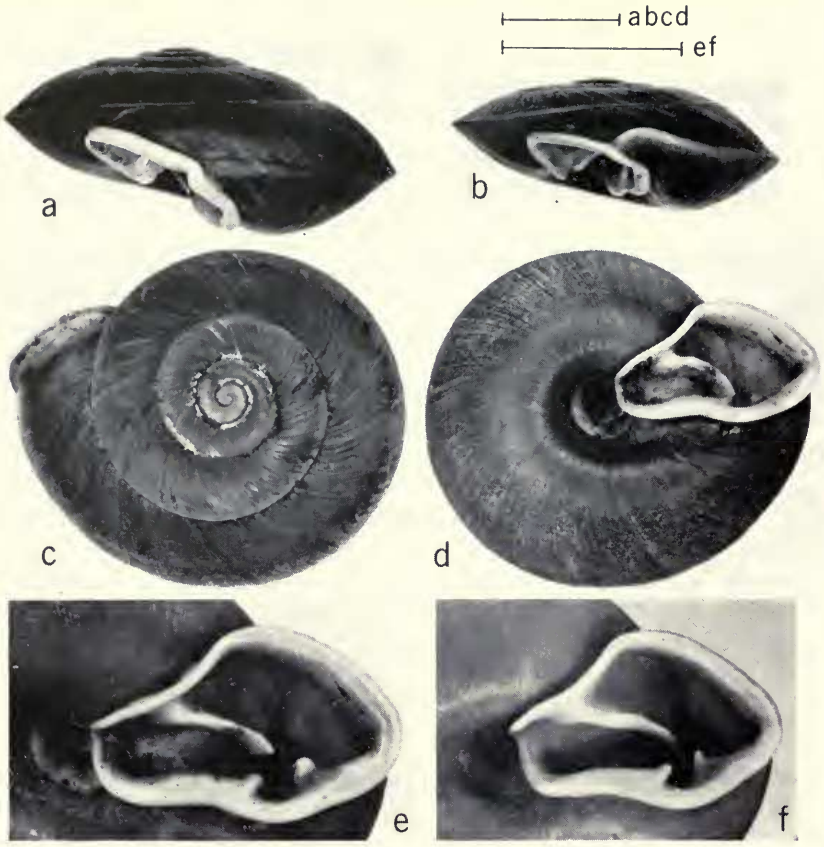


FIG. 36. Shells of: *a*, *Labyrinthus plicatus*, normal form, "Venezuela." Zurich; *b–e*, *Labyrinthus marmatensis*, Angelópolis, Antioquia, Colombia. Neuchatel. Holotype of *angelopolites* Piaget, 1912 (*b*, side; *c*, top; *d*, base; *e*, aperture); *f*, *Labyrinthus marmatensis*, Marmato, Colombia, ANSP 8913. Aperture of holotype. Scale lines equal 10 mm.

Both H. B. Baker and Wurtz (*loc. cit.*) have dissected *plicatus*, which agrees closely in anatomy with *L. otis orthorhinus*.

Labyrinthus marmatensis Pilsbry, 1910. Figure 36b–f.

Helix (*Labyrinthus*) *plicata* var. Pilsbry, 1889, Man. Conch. (2), **5**, p. 164, pl. 63, figs. 6–8—Marmato, Colombia.

Pleurodonte (*Labyrinthus*) *plicata marmatensis* Pilsbry, 1910, Proc. Acad. Nat. Sci., Philadelphia, **1910**, p. 505—Marmato, Colombia.

Labyrinthus angelopolites Piaget, 1912, Mem. Soc. neuchateloise Sci. nat., **5**, p. 258, pl. 10, figs. 1–6— Angelópolis, near Titiribí, Antioquia, Colombia at 1,970 meters elevation (Fuhrmann!).

Range.—Cauca River Valley in Colombia from Marmato to Angelópolis.

Material.—Colombia: CALDAS—Marmato (ANSP 8913, types of *marmatensis*, MCZ 154017). ANTIOQUIA—Jericó(USNM 424726); Angelópolis (Neuchatel, types of *angelopolites*); near Medellín (USNM 518435). No exact locality (Edinburgh, Zurich, CNHM 132550).

Diagnosis.—The prominent, sinuately curved parietal lamella runs diagonally into the lower parietal lip either at full height or after it starts descending; basal lip nearly straight with narrow, slanted crescentic lamella; lower palatal lip slightly concave with strong posterior indention, having a conical to spade-shaped, slightly recessed lamella; periphery acutely angulated with protruded keel; spire slightly elevated with flat or slightly rounded sides; color dark yellow brown. Diameter 26.6–37.2 mm. (mean 32.7 mm.), H/D ratio 0.318–0.428 (mean 0.363).

Remarks.—Although originally described as a subspecies of *L. plicatus*, the structure of the parietal lamella is totally different and the wide geographic separation also makes subspecific status unlikely. The original figures and descriptions of *Labyrinthus angelopolites* Piaget, 1912 are highly inaccurate and misleading. Through the kindness of Dr. Lothar Forcart, Naturhistorisches Museum, Basel, it was possible to borrow the two cotypes. They are unquestionably the same as Pilsbry's species. The slightly larger (diameter 33.7 mm.) of the two cotypes is here selected as lectotype.

Nearly all the specimens were 31–34 mm. in diameter, with only the shell found near Medellín being appreciably smaller (diameter 26.6 mm.). All of the specimens measuring more than 34 mm. in diameter were without exact locality.

Species of Uncertain Affinity

The following two species were inadequately described and figured. The few comparative remarks included are based on the descriptions and offered primarily in case new collections from the vicinity of the type localities should become available for study.

Labyrinthus euclausus Beddome, 1908

Labyrinthus euclausus Beddome, 1908, Proc. Malac. Soc. London, 8 (1), p. 20, text fig.—near Zaragoza, Colombia at 800 feet elevation in dense forests (Ernest Bell!).

Remarks.—The single figure and description are totally inadequate to enable recognition of this species. The mention of a large lower palatal tooth suggests that this is a member of the *L. otis* group, but the obvious failure of the parietal lamella to merge with the parietal lip and the only slightly sinuated basal lip prevent its association with any previously described species.

Ernest Bell was a mining engineer, hence it is more likely that the type locality is in Antioquia rather than the towns of the same name in Cauca or Valle de Cauca. If this supposition is correct, then possibly *L. euclausus* may be found to be a relative of *L. marmatensis*. The distinctive color pattern of reddish spiral bands on a yellow-white background is like *L. unciger*, but the tooth structure is obviously different from both *marmatensis* and *unciger*.

Labyrinthus sharmani (Gude, 1912). Figure 26c–d.

Ambages sharmani Gude, 1912, Proc. Malac. Soc. London, **10** (1), pp. 21–22, 2 figs.—Alejandría, 50 miles from Medellín, Colombia at 5,600 feet elevation (Sharman!).

Diagnosis.—The parietal lip is straight and markedly elevated from the wall while the parietal lamella is bifurcate—upper arm shorter and descending more gradually than the lower; basal lip moderately sinuated with a prominent knob-like lamella; lower palatal wall with single high, thick lamella; upper palatal wall with a plate-like lamella "nearly parallel with the peristome, its upper termination bent slightly forward"; umbilicus only slightly covered by basal and parietal lips; periphery rounded or obtusely angulated. Surface granulose. Diameter 21.2 mm.

Remarks.—The bifurcated parietal lamella, if not teratological, identifies this species immediately. In having a nearly straight parietal lip with simple relationship to the lamella, this species is much nearer to the *L. isodon* complex than to *vexans* or *clappi*. It may well be found to be a connecting link between the two complexes, but because of the apparent palatal teeth similarity to those found in *bogotensis* and *otostomus*, Gude's grouping may be correct. Only the type specimen in the British Museum (Natural History) (number 1912.1.27.1) is known.

The possibility exists that *sharmani* was based on abnormal individuals of the *isodon* complex.

GENUS **Isomeria** ALBERS, 1850

Die Heliceen, p. 126.

Type species.—*Helix oreas* Koch, 1844 by monotypy.

Range.—From Angelópolis and Frontino, Antioquia, Colombia south at medium elevations in the Andes to Chota District, Cajamarca, Peru, with two isolated species in the Sierra Nevada de Santa Marta, Magdalena, Colombia. A record from Ocaña in the southern part of the Sierra de Perijá is questionable, but two species are known from Villavicencio, Meta, Colombia, and a third was described from Bogotá. The largest number of species are from Ecuador, on both Amazonian and Pacific slopes. Only in the Pacific lowlands of Ecuador is a species (*I. globosa*) recorded from less than 1,500 feet elevation.

Diagnosis.—Shell small to very large (diameter 18–73 mm.); globose to helicoidal or depressed lenticular; surface sculpture of growth wrinkles, grooves, microscopic granulations, and/or heavy malleations; periphery faintly to acutely angulated, occasionally with protruding keel, usually obtusely angulated; umbilicus normally closed or very narrowly open laterally, rarely distinctly open with an internal groove visible, closure usually by extension of basal and parietal lips, sometimes by addition of an accessory plate; aperture strongly deflected in adult, lip thickened and reflected, usually with one or more small denticles, toothless in some species; parietal callus very thin to thickened with a narrow to wide raised edge, straight or evenly curved, sinuated only in *I. inexpectata;* basal and palatal lips thickened internally, evenly curved or straight; parietal wall generally toothless, occasionally with very small conical tooth or short lamella; basal lip with 0–2 small denticles, sometimes joined by a callus; lower palatal lip toothless or with a small conical lamella, very rarely with a large tooth marked by posterior indentation (*I. globosa*); upper palatal lip with 0–2 small to medium-sized denticles. In the only species that has been dissected, *I. globosa,* the jaw, radula, pallial region and genitalia show exactly the same structures found in *Labyrinthus,* with the exception of having a penial appendage as well as an epiphallic flagellum. The vagina has a ring of low knobs around the base (fig. 4c) and both penis and vagina have the small hooked denticles topping the pilasters and ridges that so far have been found only in the mainland South American camaenids.

Remarks.—Except for referring *Labyrinthus vexans* (Dohrn) and *L. aenigmus* (Dohrn) to *Isomeria,* the genus has been consistently recognized as a discrete unit, which is "confined to the high mountains of Ecuador and Colombia." The great reduction in size or total absence of the apertural teeth, which results in a widely open aperture, are in great contrast with the situation in *Labyrinthus.* Only in *Isomeria inexpectata* from the Sierra Nevada de Santa Marta and

I. minuta from Sierra de Mariquita are there species that seem to be intermediate in shell characters. The only species of *Isomeria* that has been dissected, *I. globosa*, cannot be considered typical, since it is not only the single lowland species (Pacific coast of Nariño, Colombia and Ecuador), but also the only species with a large lower palatal tooth marked by a posterior indention.

The great deflection of the aperture allows recognition of the same three apertural zones seen in *Labyrinthus*, although *Isomeria* does not have a basal tooth separating the basal and palatal lips. There is no sharp separation of these areas, but the placement of teeth is such that no confusion of basal and lower palatal teeth seems possible.

A basic shell difference between *Labyrinthus* and *Isomeria* lies in the parietal wall. In the former this is almost always an elevated lip that is often very grossly sinuated; in the latter this is a thin to thick-edged callus which is markedly sinuated only in a single species (*I. inexpectata*). The callus in *Isomeria* may have a narrow, rounded thickened edge connecting the basal and palatal lips, but it is raised to form a distinct lip with reflected edge only in the *I. subelliptica* group and *I. oreas*. Similarly, only in a very few species, *I. oreas*, *I. cymatodes*, *I. subelliptica* and some individuals of *I. continua*, is there a small crescentic to tubercular parietal lamella and only in *I. inexpectata* is there a parietal tooth of moderate prominence. The vast majority of the species have no trace of parietal dentition.

The basal lip can lack dentition, but have a heavy callus with the lip internally thickened (*I. meyeri*, *I. meobambensis* group); have a broad basal swelling or two basal teeth located one-third of the way from the umbilicus to the lower palatal lip (*I. bituberculata* group, *I. aloagana*, *I. triodonta*); a single medial tooth (*I. aequatoria*, *I. gealei*, *I. morula*); have the basal lip toothless; or have one of the above conditions so reduced by construction of a callus that the basal dentition cannot be determined (most of the remaining species). None of the species has large basal teeth.

A clear majority of the species have a conical or crescentic lamellate lower palatal tooth. All of the *I. oreas* and *I. meobambensis* groups (except the toothless *I. meyeri* and *I. scalena*), *I. inexpectata*, and three members of the *I. bituberculata* group (*I. hartwegi*, *I. medemi*, and *I. bourcieri*) have this tooth. The remaining members of the *I. bituberculata* complex and all of the *I. subelliptica* group except *I. minuta* lack a lower palatal tooth. Only in *I. globosa* is this tooth large and marked by a posterior indentation such as is found in most species of *Labyrinthus*. In the remaining species it is a small, incon-

spicuous denticle without any obvious functional significance. *I. meobambensis* is unique in having a lateral extension running from the parietal tooth to the periphery.

Upper palatal dentition is equally reduced. Small, rounded, inconspicuous knobs are rarely seen in *I. kolbergi* and *I. aequatoriana*, commonly found in *I. triodonta*, *I. juno* and *I. bituberculata*, greatly reduced in *I. inexpectata* and *I. hartwegi*, and are very large in *I. bourcieri*. In the latter species, the upper palatal tooth is distinctly larger than the lower palatal tooth. *I. gealei* and *I. aequatoria* are unique in having the peripheral groove accentuated with the lower part of the upper palatal lip forming a triangular tooth projecting into the aperture, much as in *Labyrinthus otostomus*. Apparently *I. morula* has much the same dentition as *I. bituberculata*.

Few species have the periphery as acutely angulated as is common in most *Labyrinthus*. Usually it is obtusely or only slightly angulated. Shell sculpture is quite variable, ranging from the nearly smooth surface of *I. jacksoni* to finely granulated (*I. aequatoriana*), heavily granulated (*I. stoltzmanni*), with prominent radial grooves and growth lines (*I. meobambensis*) or with heavy malleations, particularly on the body whorl (*I. cymatodes*). Each species seems to have its own particular combination of sculpture types, but these patterns are easily altered by erosion of the shell surface. Thus only slight use has been made of shell sculpture in preparing the keys, although in some cases it was the most obvious differentiating character.

Much more than in *Labyrinthus*, there is a tendency toward closure of the umbilicus. Only in *I. oreas*, *I. kolbergi*, *I. stoltzmanni*, the *I. subelliptica* group, and *I. inexpectata* can the umbilicus be said to be open. In a number of other species the umbilicus shows an open lateral crack, but in three of these—*I. cymatodes*, *I. fordiana* and *I. scalena*—there is an accessory plate of calcium that almost completes umbilical closure. Most of the species in the *I. bituberculata* group, all of the *I. meobambensis* group and *I. aequatoriana* have the umbilicus completely closed by expansion of the parietal and basal lips.

One of the more striking shell variations concerns the tendency toward lateral compression of the last one-quarter to one-third of the body whorl. This produces a very distinct alteration in shell outline from an evenly coiled, circular form to an asymmetrical, ellipsoidal pattern seen in, among others, *I. oreas*, *I. scalena*, *I. basidens gudeana* and *I. stoltzmanni*. This is not confined to a particular group of species, but appears, to a greater or lesser extent, within each group. The functional significance of the lateral compression is unknown.

While a rather limited size range may be characteristic of any particular species, the presence of obviously dwarfed populations and occasional very large examples in almost every species for which more than a few examples were available, means that size is often of little use or a very misleading aid toward identification. For this reason, and since the positive shell characters separating species are fewer than in *Labyrinthus*, the mean size of all adult specimens together with the range in size has been given for each species. These figures are only general indications of size, since the material available was often strongly biased by the presence of a large sample of a dwarfed population (*I. aequatoriana*) or by scattered material from both large and small populations (*I. oreas*).

Classification of *Isomeria*

The great reduction in apertural dentition eliminates the most useful set of shell characters for grouping species. Delineation of species groups in *Isomeria* has been based on apparently clumped tendencies in respect to size, shape, sculpture and umbilical closure. Intragroup variability is sufficiently large that concise diagnoses of the species groups are impossible.

Although its shape and size are very close to those of the *I. bituberculata* complex, its striking tooth development and isolated geographic range are such that *I. inexpectata* is clearly separable. The *bituberculata* group shows a depressed-globose form, closed or slightly angled periphery and relatively small size. *I. hartwegi* is greatly modified in form and apertural dentition, but seems nearest to this group. A moderate contrast is seen in the *I. subelliptica* group with the umbilicus widely open for *Isomeria* and the very reduced dentition. Most of the species are larger in size than either of the first two groups.

The *I. meobambensis* group has the umbilicus completely closed by expansion of the parietal callus and basal lip and the species are of medium size. That the *I. oreas* complex is a natural group seems dubious. Although most species have a narrowly to widely open umbilicus and show minor variations in shell features that seem clinal from species to species, three species (*I. cymatodes, I. fordiana* and *I. scalena*) show a peculiar form of umbilical closure, *I. aequatoriana* has the umbilicus closed as in the *I. meobambensis* group, and *I. globosa* has very strongly developed lower palatal dentition.

The species groups are more combinations for convenience in identification and study than any reasoned attempt at classification. There is simply too little evidence available to allow construction of

a phylogeny. As in *Labyrinthus*, the working assumption has been made that a grouping proceeding from the smaller to the larger may reflect some natural affinities. It is reasonable to hope that study of the soft parts will provide data toward a phylogenetic classification and particularly toward clearing up the currently insoluble problem of the single versus multiphyletic affinities of *Isomeria* and *Labyrinthus*.

Three specific names, *I. calomorpha*, *I. fauna* and *I. equestrata*, could not be identified from the original figures and descriptions. Only one of them was represented in collections and the specimens could be *I. kolbergi* (see p. 174). They are probably synonyms of other species, but cannot be identified at this time and are listed as *nomina dubia* (pp. 193–195).

There is sufficient variability in the number and position of the teeth, degree of umbilical closure, peripheral angulation and size that construction of a key to the species groups is exceedingly difficult. Typical examples of any species can be easily placed, but the range of variation makes the keying of odd individuals hazardous. The following key has attempted to allow for the known range of variation, but subsequent collections probably will make it inoperable.

REVIEW OF THE SPECIES

KEY TO THE SPECIES GROUPS OF *ISOMERIA*

1. Parietal tooth absent or very small and not merging with sinuated edge of parietal callus.....2
   Parietal tooth large, merging with edge of sinuated parietal callus.
   Group of *Isomeria inexpectata* new species
2. Umbilicus closed to moderately open, but if opening more than just a narrow crack, having a lower palatal tooth and diameter more than 20 mm.....3
   Umbilicus broadly open, only slightly narrowed by extension of basal and parietal lips; lower palatal tooth absent, or if present, diameter less than 20 mm.
   Group of *Isomeria subelliptica*
3. Umbilicus completely closed by extension of basal and parietal lips, diameter less than 42 mm.; OR with a slight lateral umbilical crack, periphery very obtusely angulated, diameter less than 35 mm. and lower palatal tooth absent.....4
   Umbilicus at least slightly open, OR with closure affected by construction of a secondary plate, OR if completely closed by extension of lips, then shell more than 43 mm. in diameter.....Group of *Isomeria oreas*
4. Diameter 30–42 mm., specimens with no apertural teeth or swellings, OR a single lower palatal tooth with an upward lateral extension (fig. 47b), OR both a lower palatal tooth and a *smaller* upper palatal tooth located near a *right* or *acutely* angled periphery.....Group of *Isomeria meobambensis*
   Diameter under 30 mm.; OR having basal swellings or teeth, but no lower palatal tooth; OR with very obtusely angulated periphery and upper palatal tooth distinctly larger than lower palatal tooth.
   Group of *Isomeria bituberculata*

Group of *Isomeria inexpectata*

The single species from the isolated Sierra Nevada de Santa Marta shows affinities to both *Isomeria* and *Labyrinthus*. It tentatively has been placed in *Isomeria*, but differs from all other species groups in having a relatively large parietal lamella that runs into the raised edge of a *sinuated* parietal callus.

Isomeria inexpectata, new species. Figure 37a–d.

Diagnosis.—A small (diameter 23.3–24.6 mm.) species of *Isomeria* immediately separable in having a distinctly lamellar parietal tooth that fuses with the lower part of the raised parietal callus. Form, color and general appearance are much as in *I. basidens* and *I. bituberculata*. The latter two differ in having the two basal teeth very close together, while in *I. inexpectata* they are widely separated. The moderately prominent lower palatal knob and faint trace of an upper palatal tooth also separate *I. inexpectata* from *Isomeria medemi*.

Holotype.—United States National Museum number 599522. Siminchucua River, between San Sebastián de Rábago and Mamancanáca, 8,500–9,000 feet elevation, headwaters of Rio Fundación, south slope of Sierra Nevada de Santa Marta, Magdalena, Colombia. Collected by M. A. Carriker from February 1–10, 1946.

Description.—Shell small, depressed globose, with 4½ normally coiled whorls. Spire moderately elevated, flatly rounded above, H/D ratio 0.569. Apex and early spire worn, without trace of distinctive sculpture. Lower whorls with weak radial growth lines, but no malleations or granulations. Periphery faintly angulated with a lighter color zone. Color reddish brown with numerous greenish-yellow flecks, especially numerous above periphery. Lip white, without any brownish tint. Umbilicus very narrowly open, partly closed by extension of basal and parietal lips, contained 17.6 times in the diameter. Aperture ovate, only slightly deflected, inclined about 40° from the shell axis. Parietal wall with single crescentic lamella running into lower parietal callus. No raised parietal lip, but a heavy sinuated lower parietal callus extending from fusion with parietal lamella to umbilicus; upper parietal wall with faint trace of a broad callus, much reduced from lower parietal callus. Basal lip thickened, narrowly reflected, with two inconspicuous, rather widely separated knobs. Lower palatal lip with a prominent, triangular, raised knob. Upper palatal lip with a faint trace of a tooth located just on the periphery. Height of holotype 14.0 mm., diameter 24.6 mm.

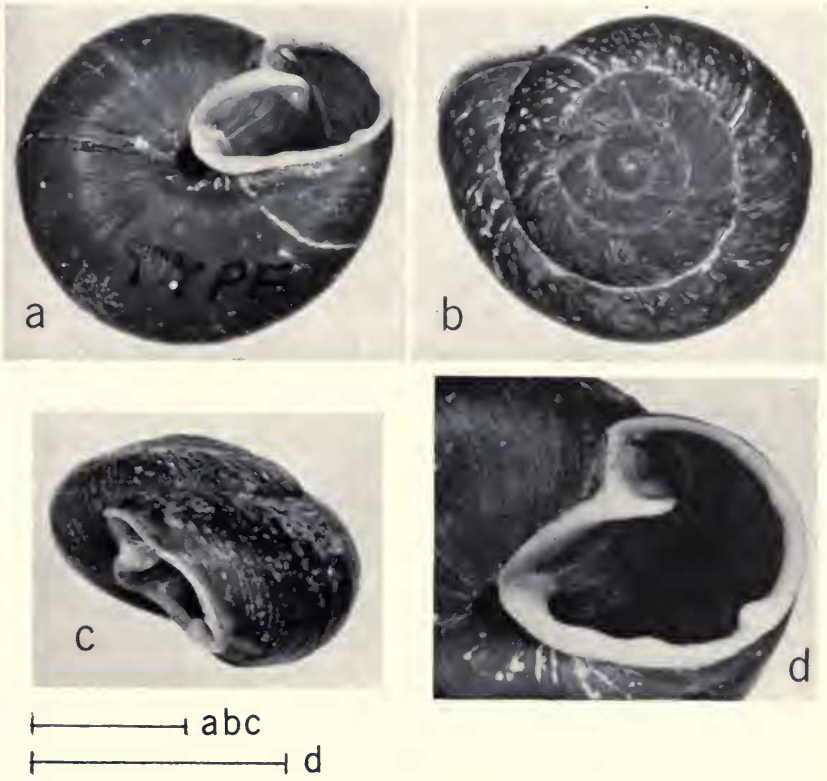


FIG. 37. *Isomeria inexpectata:* Siminchucua River, Sierra Nevada de Santa Marta, Colombia, USNM 599522. Holotype (*a–c*), paratype (*d*). (*a*, base; *b*, top; *c*, side; *d*, aperture). Scale lines equal 10 mm.

Range.—Known only from the type locality.

Paratypes.—USNM 599522, CNHM 132554.

Remarks.—While the general appearance of the shell is unquestionably that of the *bituberculata* group of *Isomeria*, even casual inspection of the teeth shows important differences. No other species of *Isomeria* has such a distinct parietal lamella. A few have a small, circular or elongated, raised callus on the parietal wall, but none has a lamella. Furthermore, the raised parietal callus edge in *Isomeria* is straight or slightly curved. In *I. inexpectata* the parietal callus has the same sinuated shape seen in the more complexly toothed members of the *Labyrinthus isodon* complex. As in that group, the parietal lamella of *I. inexpectata* fuses directly with the lower portion of the parietal callus, with the upper portion being greatly reduced in

size. Furthermore, in the *I. bituberculata* complex, the two basal lip teeth are usually very close together or actually fused and elevated on a slight ridge (see fig. 40). Only in *I. medemi* are they widely separated. In *I. inexpectata*, the basal lip has two widely separated, low swellings with the outer located in the normal position of the basal tooth in *Labyrinthus*. The lower palatal wall of *I. inexpectata* has a prominent raised knob and there is a faint trace of a swelling on the periphery.

The structure of the apertural teeth is precisely what would be expected if *Labyrinthus vexans* or *L. isodon* had the tooth size greatly reduced, and is rather similar to the Caracas form of *L. leucodon*. It is quite different in size and tooth position from *I. medemi* and its relatives, although the shell shape and color are precisely as in *I. bituberculata*. Furthermore, the Sierra Nevada de Santa Marta is far removed from the primary distribution of *Isomeria*. *Isomeria oreas* has been found at Angelópolis, Antioquia and *I. continua* from the area around Bogotá, but neither of these is at all similar in appearance. *I. bituberculata* and its allies are primarily found in Ecuador, with *I. neogranadensis* from the Caldas–Tolima border region, *I. basidens* described from "Bogotá," and only *I. medemi* is known from the Sierra Nevada de Santa Marta.

Available data is obviously inadequate to tell whether *I. inexpectata* represents a local *Isomeria*-like derivative of *Labyrinthus* in the Sierra Nevada de Santa Marta, or whether it has phyletic relationships with other *Isomeria* from southern Colombia and Ecuador. Because of its altitudinal range, 8,500–9,000 feet, general appearance as an *Isomeria*, presence of *I. medemi* in the same range, and dissimilarity in tooth structure to the *Labyrinthus* of the Sierra Nevada de Santa Marta (*L. clappi* and *L. sieversi*), I have arbitrarily placed *I. inexpectata* in *Isomeria*.

Only three specimens are known of this very intriguing species. Size and shape variation is summarized in Table XIII. One paratype contained remnants of the soft parts. Softening in trisodium-phosphate revealed that only the foot, mantle collar and an encysted nematode had escaped the attention of dermestid beetle larvae. These structures, at our present level of knowledge, yield no data on generic classification.

Group of *Isomeria bituberculata*

These are small to medium sized species (diameter 20–36 mm.) with either a prominent basal lip swelling or two basal teeth, the pe-

riphery usually obtusely angulated, the umbilicus completely closed or at most narrowly open laterally, no parietal tooth present, and often with the last part of the body whorl moderately constricted.

The species are sufficiently similar to justify grouping, although *I. hartwegi* could be considered a dwarf member of the *I. meobambensis* group. Possibly two weakly differentiated series of species could be recognized. The Colombian *I. basidens* and *I. neogranadensis* have a broad low basal lip swelling and no other teeth, while the Ecuadorean shells and the single species from the Sierra Nevada de Santa Marta have a pair of basal teeth and other denticles. *I. basidens* is smaller and with a more obtusely angled periphery than *I. neogranadensis*. *I. medemi* has two rather widely set basal teeth and a small lower palatal tooth, but no trace of an upper palatal tooth. *I. hartwegi* has a nearly right angled periphery, small lower palatal tooth, and an evenly elevated spire. It is a much thinner shell than the large, heavy, obtusely angulated *I. juno*, which lacks the lower palatal tooth. Probably *I. juno* is most closely related to *I. bituberculata*, which differs in its more globose shell, less angulated periphery and thinner shell and lips. Finally, *I. bourcieri* has a color pattern duplicated only by *Labyrinthus magdalenensis*, a lower palatal tooth, and an upper palatal tooth that is larger than the lower one.

Data on two of the three Colombian species is much too fragmentary to allow delineation of their geographic ranges. The third, *I. medemi*, is known from two examples. Of the Ecuadorean species, *I. bourcieri*, *I. bituberculata* and *I. juno* have been reported from the same areas (Upper Río Esmeraldas, Napo and Pastaza drainages), but with no data as to ecology. There are no cited elevations for *I. juno* and only two (8,200 feet) for *I. bourcieri*. The several cited elevations for *I. bituberculata* lie between 3,900–13,000 feet. Localities without elevation data range much lower, reaching 1,680 feet at Napo. These are regional citations, of course, and give no indication of true altitudinal range. *I. hartwegi* has a much more southern range, having been reported from 3,000 feet elevation in the Catamayo Valley north to Cuenca (8,400 feet) and then in lowland areas of the Pacific drainage near Guayaquil (Cerritos de Taura and La Galia, Yaguachi).

KEY TO THE *ISOMERIA BITUBERCULATA* GROUP

1. Basal lip with a small to prominent swelling 2
   Basal lip with one or more teeth, occasionally partly obscured by a callus 5
2. Shell surface without malleations 4
   At least part of shell surface with malleations 3

3. Malleations on lower part of body whorl; Sierra Nevada de Santa Marta. *I. medemi* new species
   Upper part of spire malleated; Cauca..... *I. basidens gudeana* (Ancey, 1904)
4. Basal swelling very small; diameter 34 mm.... *I. neogranadensis* (Pfeiffer, 1845)
   Basal swelling moderately prominent; diameter 24 mm. *I. basidens basidens* (Mousson, 1873)
5. A lower palatal tooth present.....6
   No lower palatal tooth present.....7
6. Periphery right angled; upper palatal tooth weak or absent; color brown. *I. hartwegi* (Pfeiffer, 1846)
   Periphery obtusely angulated to rounded; color reddish brown with yellow markings; upper palatal tooth larger than lower palatal tooth. *I. bourcieri* (Pfeiffer, 1853)
7. Teeth reduced in size; periphery right angled with lighter color band; lip and callus very thick..... *I. juno* (Pfeiffer, 1850)
   Teeth larger and lip thinner; periphery obtusely angulated to rounded without a lighter color band..... *I. bituberculata* (Pfeiffer, 1853)

Isomeria medemi, new species. Figure 38a–d.

Diagnosis.—A rather small (diameter 25.7–28.2 mm.) species of *Isomeria* with two prominent basal teeth, a small lamellar lower palatal tooth, closed umbilicus and obtusely angulated periphery. *I. inexpectata* differs in having a parietal lamella and open umbilicus. The nearest relatives seem to be in the *I. bituberculata* complex, but all of these have less prominent basal teeth, lack the lower palatal tooth or have a more depressed form.

Holotype.—Chicago Natural History Museum number 133261. Finca La Granja, San Lorenzo Ridge, Sierra Nevada de Santa Marta, Magdalena, Colombia at 8,200–8,850 feet elevation. Collected by Carlos Alberto Velásquez and Fred Medem from February 19–25, 1964.

Description.—Shell rather small, somewhat depressed globose, with slightly less than 4½ normally coiled whorls. Spire elevated, slightly flattened on apex, nearly flat laterally, H/D ratio 0.604. Shell very worn, with only faint traces of radial ribbing remaining. Last part of body whorl showing marked malleations. Periphery obtusely angulated, becoming rounded on last one-third of body whorl. Periostracum and color completely worn off shell. Umbilicus completely closed by expansion of basal and parietal lips. Aperture ovate, moderately deflected, inclined about 45° from the shell axis. Parietal wall with prominent callus, edge slightly sinuated. Basal lip with two rather widely spaced, prominent teeth, outer one slightly larger. Lower palatal lip with small, crescentic lamellar tooth, relatively narrow and not extending posteriorly. Upper pal-

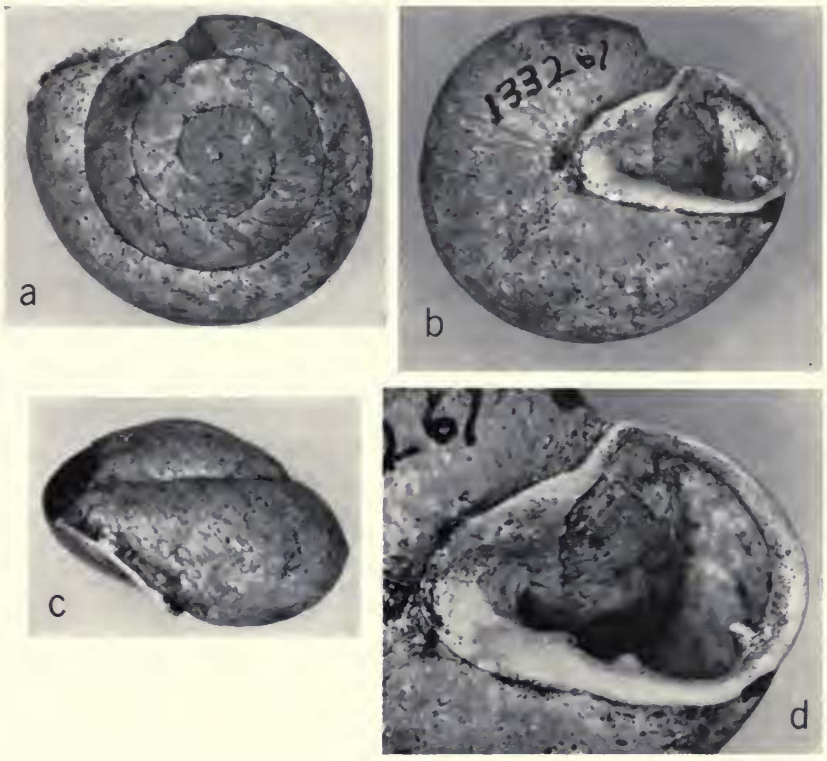


FIG. 38. *Isomeria medemi:* Finca La Granja, San Lorenzo, Sierra Nevada de Santa Marta, Colombia, CNHM 133261. Holotype (*a*, top; *b*, base; *c*, side; *d*, aperture).

atal lip without dentition, only slightly reflected at upper margin, becoming more sharply reflected with posterior gutter near periphery. Lower palatal lip strongly reflected. Basal lip recurved, appressed to basal margin. Height of holotype 17.0 mm., diameter 28.2 mm.

Paratype.—CNHM 145160 from the type locality.

Remarks.—Description of this species from two dead, partly broken shells is warranted only because of the light it sheds on the relationships of *I. inexpectata*. By confirming the development of "typical" *Isomeria* in the Sierra Nevada de Santa Marta, *I. medemi* gives a firmer basis for placing *I. inexpectata* in this genus rather than in *Labyrinthus*.

The type locality of *I. medemi* is located on the same northwest spur of the mountain mass as is *L. clappi*. The latter is known only

from 4,000–5,000 feet elevation, while the types of *I. medemi* were taken at 8,200–8,850 feet elevation. *I. inexpectata* is known from 8,500–9,000 feet elevation on the southwest face of the main Sierra, at least 50 air miles from the San Lorenzo spur. The other camaenid described from the Sierra Nevada de Santa Marta, *L. sieversi*, has been found in the center of the north face at 5,500 feet (San Miguel), the northeast spur of the mass at 2,500 feet (Los Gorros) and at 330–670 feet (Oblo), whose exact locale is not known to me.

The relationships of *I. medemi* are unquestionably with the *bituberculata* complex. It is easily distinguished by its isolated geographic range, larger basal teeth, single lower palatal tooth and elevated shape. The other two Colombian species, *I. basidens* and *I. neogranadensis*, lack a lower palatal tooth, while all the Ecuadorean species obviously have different tooth size and numbers.

This species is named after one of its collectors, Dr. Fred Medem, who has contributed so much to knowledge of the Colombian fauna.

Isomeria basidens basidens (Mousson, 1873). Figures 39a–c, 40a.

Helix basidens Mousson, 1873, Malak. Blätt., **21**, pp. 2–3—Bogotá (Wallis!); Pfeiffer, 1876, Novit. Conch., **4**, pp. 118–119, pl. 127, figs. 7–9; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 362.

Helix (*Isomeria*) *basidens* Mousson, Pilsbry, 1889, Man. Conch. (2), **5**, p. 154, pl. 48, figs. 52–54.

Pleurodonte (*Isomeria*) *basidens* (Mousson), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Known only from the type collection.

Material.—Colombia: CUNDINAMARCA—Bogotá (Zurich, holotype of *basidens* Mousson).

Diagnosis.—Basal lip with a moderately prominent swelling; umbilicus closed; lip slightly brown tinted; parietal callus very thin, edge not elevated; surface with very fine granulations and growth striae, but no malleations; periphery very obtusely angulated. Diameter 25.4 mm.

Remarks.—The smaller size, less sharply keeled periphery, more prominent basal lip swelling and weaker surface sculpture easily separate *basidens* from *neogranadensis*. Subspecies *gudeana* has the basal lip swelling much more prominent and is malleated on the upper spire (see fig. 39d). The type locality "Bogotá" could mean anywhere within a 100-mile radius of the city. No more recent material has been collected. The type specimen measures 14.2 mm. high, diameter 25.4 mm., H/D ratio 0.559, with 4⅛ whorls.

The slightly larger *I. medemi* differs in having two rather widely separated basal teeth and a lower palatal tooth.

Isomeria basidens gudeana (Ancey, 1904). Figures 39d–e, 40b.

Helix (Isomeria) neogranadensis var., Dunker, 1882, Jahr. d. Malak. Gesell., **9**, pp. 377–378, pl. 11, figs. 5–6—locis uliginosus, Ecuador; Pilsbry, 1889, Man. Conch. (2), **9**, p. 153, pl. 62, figs. 22–23; Kobelt, 1894, Syst. Conch. Cab., I (12), **4**, p. 694, pl. 198, figs. 5–6.

Pleurodonte gudeana Ancey, 1904, Jour. de Conchy., **52**, p. 297—based on figures in Kobelt (*loc. cit.*).

Pleurodonte (Isomeria) gudeana (Ancey), Pilsbry, 1926, Proc. Acad. Nat. Sci., Philadelphia, **78**, pp. 4–5, pl. 2, figs. 1–3—either La Cumbre, Cordillera Occidental, Prov. El Valle or mountains east or west of Popayán, Prov. Cauca, Colombia.

Pleurodonta (sic) basidens rugospira n. subsp., Pilsbry, 1926, *op. cit.*, 78, p. 15—in explanation of Plate 2 for figs. 1–3, referred to in text as *P. gudeana* Ancey, 1904.

Range.—Probably Central Cauca, Colombia.

Material.—Colombia: CAUCA—Popayán (ANSP 132449, CNHM 78831); Volcan de Puracé, Paletará (R. Wright Barker, CNHM 132553). "Ecuador" (SMF 26347).

Diagnosis.—Basal lip with a prominent swelling; umbilicus closed; outer lip slightly tinted; parietal callus nearly absent; upper part of spire with heavy malleations, lower part with weak malleations and very fine granulations; periphery very obtusely angulated. Diameter 25.6–29.6 mm., H/D ratio 0.599–0.625.

Remarks.—The more prominent basal lip swelling, slightly distorted form of coiling and the presence of marked malleations on the upper spire at once separate *gudeana* from *basidens*. They are considered subspecies in view of their general similarity, but could be found to be specifically separable. Both sets of *gudeana* have the malleations clearly visible for the first 2¼–2½ whorls, gradually being replaced by the very fine granulations found on the lower spire and shell base. *I. medemi* differs in having the malleations appear near the periphery on the last half of the body whorl. Size variation of *I. b. gudeana* in the three adults with exact locality data is minor, height 15.5–16.1 mm., diameter 25.6–26.9 mm., H/D ratio 0.599–0.615, with 4–4¼ whorls.

The Paletará Valley is between 8,850–11,200 feet elevation, while La Cumbre and Popayán are between 5,150–5,775 feet elevation. Neither set of specimens has data as to the elevation from which the specimens were taken, so that the altitudinal range is unknown. All of the possible localities are in the upper Cauca drainage.

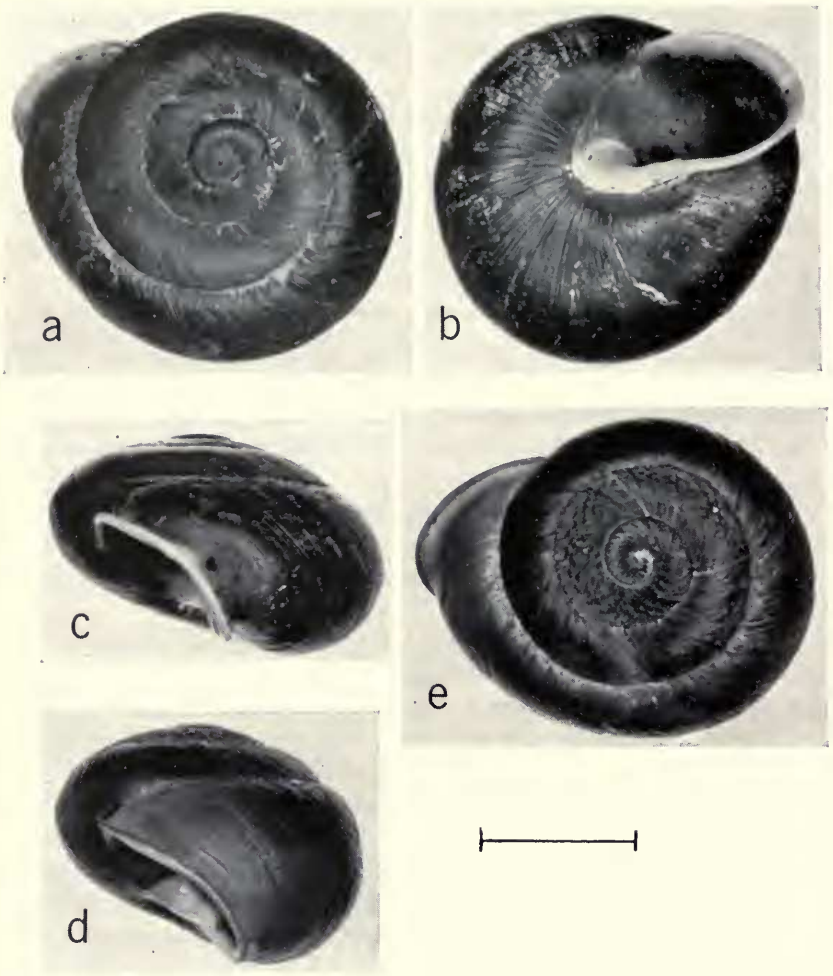


FIG. 39. *Isomeria basidens: a–c, Isomeria basidens basidens*, Bogotá, Colombia. Zurich. Holotype (*a*, top; *b*, base; *c*, side); *d–e, I. b. gudeana*, La Cumbre, Colombia, CNHM 78831 (*d*, top; *e*, side). Scale line equals 10 mm.

Isomeria neogranadensis (Pfeiffer, 1845). Figures 40c, 41a–c.

Helix neogranatensis (*sic*), Pfeiffer, 1845, Proc. Zool. Soc. London, **1845**, p. 64 —Quendeu Mt., Colombia.

Helix neogranadensis Pfeiffer, 1848, Monog. helic. viv., **1**, p. 296; Reeve, 1852, Conch. Icon., *Helix*, pl. 99, fig. 548; Pfeiffer, 1853, Monog. helic. viv., **3**, p. 206; Pfeiffer, 1854, Syst. Conch. Cab., I (12), **3**, pp. 435–436, pl. 151, figs. 13–14 (plate issued in 1853); Pfeiffer, 1876, Monog. helic. viv., **7**, p. 358.

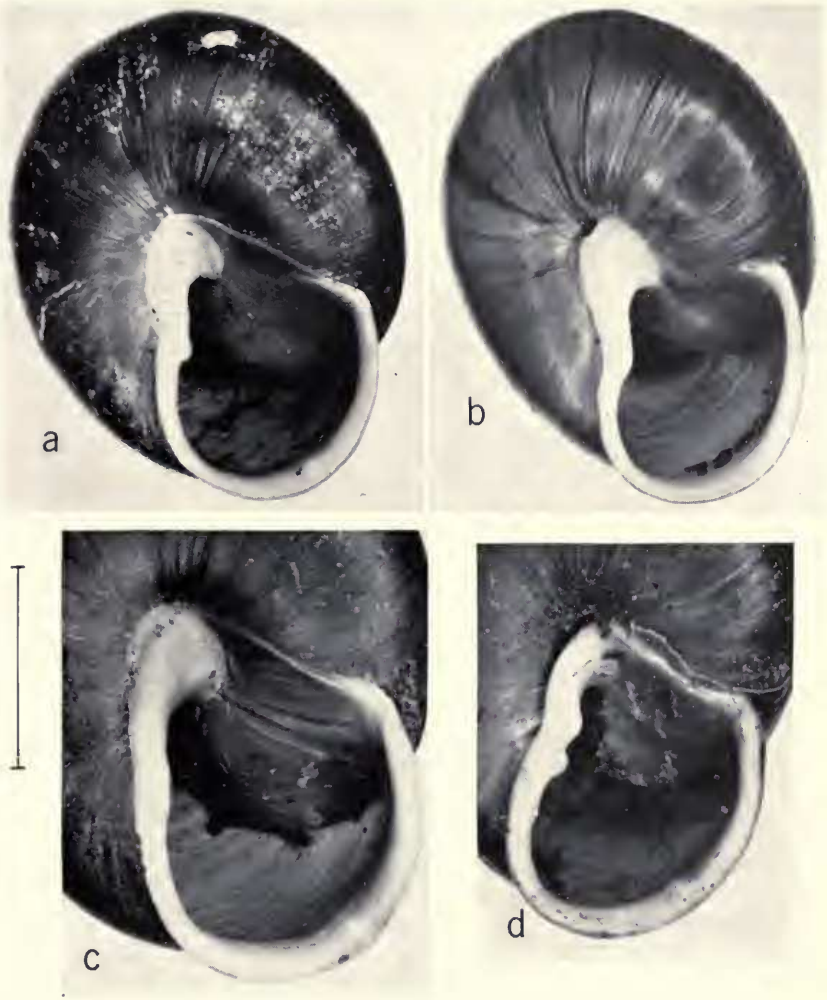


FIG. 40. Apertures of: *a*, *Isomeria basidens basidens*, Bogotá, Colombia. Zurich. Holotype; *b*, *Isomeria b. gudeana*, La Cumbre, Colombia, CNHM 78831; *c*, *Isomeria neogranadensis*, "New Granada." Zurich. Probably a paratype; *d*, *Isomeria bituberculata*, Baños, Tungurahua, Ecuador, CNHM 117842. Scale line equals 10 mm.

Helix (*Isomeria*) *neogranadensis* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 153, pl. 48, figs. 40–42.

Pleurodonte (*Isomeria*) *neogranadensis* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Known only from the type locality.

Material.—"New Granada" (Zurich, ex Mousson, Marg(?raf), 1845, probably a paratype.

Diagnosis.—Basal lip with a very faint swelling; umbilicus closed; lip flesh tinted; surface without malleations, but with fine granulations; periphery slightly to obtusely angulated; parietal callus very thin with a faint raised edge. Diameter 34 mm.

Remarks.—The larger size, more angulated periphery, and reduced basal lip swelling are the main characters separating *basidens* and *neogranadensis*. The single specimen examined is more sharply keeled than the specimen figured by Pfeiffer (*loc. cit.*) and much more sharply carinated than the specimen figured by Reeve (*loc. cit.*). It is 33.7 mm. in diameter, 17.1 mm. in height, H/D ratio 0.507, with 4½ whorls.

The type locality "Quendeu Mt." probably refers to the area of the Central Andes between Párama de Barragán and Nevado del Quindió in the Caldas–Tolima border area.

Isomeria bituberculata (Pfeiffer, 1853). Figures 40d, 41d.

Helix bourcieri Reeve, 1852 (not Pfeiffer, 1853), Conch. Icon., *Helix*, pl. 99, fig. 545—Otoralo (=Otavalo) (error), Ecuador (Bourcier!) (issued in May, 1852); error in labeling.

Helix bituberculata Pfeiffer, 1853, Monog. helic. viv., **3**, p. 242; Pfeiffer, 1854, Proc. Zool. Soc. London, **1852**, p. 153—near Tunguragua, Ecuador (Bourcier!) (issued June 27, 1954); Pfeiffer, 1854, Syst. Conch. Cab., I (12), **3**, p. 369, pl. 139, figs. 14–15 (plate issued in 1852); Pfeiffer, 1859, Monog. helic. viv., **4**, p. 292; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 383; Hidalgo, 1870, Moluscos del Viaje al Pacifico, pp. 14–15— Quito, Ecuador (Paz and Martinez!); Pfeiffer, 1876, Monog. helic. viv., **7**, p. 442; Dohrn, 1879, Jahrb. d. Malak. Gesell., **6**, p. 186; Hidalgo, 1893, Obras Malac., **3**, pp. 80, 176.

Helix (*Isomeria*) *bituberculata* (Pfeiffer), von Martens, 1860, Die Heliceen, 2nd ed., p. 156; Pilsbry, 1889, Man. Conch. (2), **5**, pp. 154–156, pl. 47, figs. 36–38; Reibisch, 1896, Abhl. naturwiss. Gesell. Isis, Dresden, **7**, p. 55—San Rafael, Tunguragua, Ecuador at 9,000 feet elevation (Wolf!); Germain, 1907, Bull. Mus. National hist. nat., Paris, **13**, p. 54—Mindo, Ecuador (Rivet!).

Dentellaria bituberculata (Pfeiffer), Miller, 1878, Malak. Blätt., **25**, p. 165—Nanegal (Wolf!).

Dentellaria tridentula Miller, 1878, Malak. Blätt., **25**, p. 165, pl. 7, figs. 5a–c—Nanegal (Wolf!), Val de Pilatón (Boetzkes!), Ecuador.

Dentellaria latidentata Miller, 1878, Malak. Blätt., **25**, p. 166, pl. 8, figs. 1a–c—Nanegal, Ecuador (Wolf!).

Isomeria bituberculata (Pfeiffer), Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 256—San Antonio, trail from Quito to Gualea, Ecuador (Cousin!).

TABLE XIII.—Size and shape variation in *Isomeria inexpectata*, *I. juno*, *I. bituberculata* and *I. meobambensis*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
I. inexpectata													
USNM 599522; Siminchucua, Colombia	3	13.9	13.6–14.0	0.13	23.7	23.3–24.6	0.43	0.585	0.569–0.601	0.009	14.9	11.6–17.6	1.76
I. juno													
CNHM 72349; Oriente Province, Ecuador	15	19.4	16.6–21.3	0.31	31.9	29.8–33.9	0.29	0.608	0.532–0.657	0.009			
USNM 628798; El Oriente, Ecuador	9	20.0	16.7–22.9	0.72	32.5	30.4–35.6	0.57	0.605	0.513–0.653	0.015			
Jackson 6998; Mera, Ecuador	6	19.6	19.1–20.5	0.21	33.5	32.8–33.9	0.19	0.586	0.564–0.606	0.007			
Jackson 6997; Puyo, Ecuador	5	19.7	19.5–20.1	0.10	33.9	33.3–34.9	0.33	0.582	0.570–0.590	0.004			
I. bituberculata													
Jackson 9668; Mera, Ecuador	4	14.7	13.7–15.4	0.37	23.7	23.2–24.0	0.19	0.623	0.583–0.665	0.017			
MCZ 65724; Guama Hill, Ecuador	4	16.1	14.1–18.3	0.99	26.4	22.5–29.4	1.68	0.611	0.585–0.632	0.011			
I. meobambensis													
ANSP 184497; Peru	5	17.6	17.0–19.4	0.46	33.9	32.8–35.3	0.46	0.518	0.482–0.562	0.013			

Isomeria latidentata (Miller), Cousin, 1887, *loc. cit.*, **12**, p. 257—San Antonio, Travenia, Ecuador (Cousin!).

Isomeria tridentula (Miller), Cousin, 1887, *loc. cit.*, **12**, p. 257—Alaspungo, trail from Quito to Gualea and trail from Aloag to Chones, Ecuador (Cousin!).

Helix (*Isomeria*) *bituberculata* var. *tridentula* (Miller), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 155–156, pl. 43, figs. 43–45.

Helix (*Isomeria*) *bituberculata* var. *latidentata* (Miller), Pilsbry, 1889, Man. Conch. (2), **5**, p. 156, pl. 43, figs. 50–52.

Pleurodonte (*Isomeria*) *bituberculata* (Pfeiffer, not Reeve), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Helix (*Isomeria*) *bourcieri* (Reeve), Germain, 1910, Miss. Arc de Méridien équatorial, **9** (3), pp. C.19–C.20—Mindo, Ecuador (Rivet!).

Range.—Central Ecuador; rather widely distributed in the Upper Río Esmeraldas drainage on the Pacific slope and the Río Napo and Río Pastaza on the Amazonian slopes. The few reported elevations are between 3,900–13,100 feet.

Material.—Ecuador: Chimborazo (CNHM 78832, ANSP 106859); "Quito" (CNHM 95505, CNHM 102457, ANSP 1460, ANSP 33138, Zurich, ZMA, SMF, Edinburgh); Mera, Oriente Prov. (CNHM 86666, Jackson 9549, Jackson 9668, CNHM 117845, CNHM 117846, ANSP 227903, Jackson 5727); Napo (CNHM 117844, Jackson 6138, Jackson 9550); Baños, Tungurahua Prov. (CNHM 117842, CNHM 117843, Jackson 6251); Nanegal (ANSP); Río Nanegal at 1,200 meters (SMF 156319); Mindo (ANSP 189040); Puyo (Jackson 9339); Ibarra (Jackson 9736); San Fernando (Jackson 7507); Topo (Jackson 9989); Mt. Tungurahua, 4,000 meters (MCZ 113918); Guama Hill, Baños, 2,000 meters (MCZ 139814, MCZ 65724); Chaupi, Mt. Tungurahua (MCZ 195502).

Diagnosis.—Basal lip with two teeth set close together, occasionally obsolete, usually small, sometimes prominent; upper palatal lip often with a very small conical tooth; umbilicus rarely closed, but usually narrowly open; periphery rounded to very obtusely angulated; lip with brownish tinge above periphery. Diameter 20–33 mm. (mean 26.3 mm.), H/D ratio 0.546–0.715 (mean 0.618).

Remarks.—This species is highly variable in dentition, size and umbilical opening, but available material is insufficient to evaluate the importance of these features.

Two variants have been named. Both were collected by Wolf near Nanegal, but it is not known if they are ecotypes or extreme variants in one population. Form *tridentula* (diameter 28 mm.) has a closed umbilicus and a small upper palatal tooth; form *latidentata* (diameter 32 mm.) has the basal teeth prominent and connected by

a ridge, a large upper palatal tooth, and a moderately open umbilicus; typical *bituberculata* (diameter 22 mm.) has two small basal teeth and a nearly closed umbilicus. Most specimens are not referable to one of the three named variations, but are intermediate in nature.

Size varied from 20–33 mm., covering the range of the types of all three named forms. No large sets of localized material were available, but even in the small sets (see Table XIII) great size and shape variation can be observed. Museum shells show a clearly bimodal distribution of diameters (see below), but no such variation in obesity index. Quite possibly *bituberculata* will eventually be split into local races or ecologic forms, but present data is inadequate for subspecific treatment.

	Diameter in mm.								
	20.7	22.2	23.7	25.2	26.7	28.2	29.7	31.2	32.7
No. of specimens	1	20	18	13	4	6	14	12	5

	H/D ratio							
	0.538	0.563	0.588	0.613	0.638	0.663	0.678	0.713
No. of specimens	1	11	16	22	24	16	2	1

The problem of Reeve's switch of the figures and descriptions of *bourcieri* and *bituberculata* is discussed under *I. bourcieri*. For the sake of nomenclatural stability, I have utilized Pfeiffer's concept of the species and consider that the figures in the *Conchylien Cabinet* represent the type form of *bituberculata*.

The rather similar *I. basidens basidens* differs in being more depressed with only a basal swelling and a less indented umbilical area.

The few elevation records, 3,900–13,100 feet, probably cover only the upper part of the altitudinal range.

Isomeria juno (Pfeiffer, 1850). Figures 41e, 42a.

Helix juno Pfeiffer, 1850, Zeits. f. Malak., **7** (5), pp. 66–67—Andes of Colombia; Reeve, 1852, Conch. Icon., *Helix*, pl. 99, fig. 547; Pfeiffer, 1853, Monog. helic. viv., **3**, pp. 208–209; Pfeiffer, 1853, Syst. Conch. Cab., I (12), **3**, pp. 304–305, pl. 127, figs. 4–5 (plate issued in 1852); Pfeiffer, 1859, Monog. helic. viv., **4**, p. 242; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 315; Hidalgo, 1870, Moluscos del Viaje al Pacifico, pp. 13–14, pl. 1, figs. 6–7—Napo and Baeza, Ecuador (Martinez!); Pfeiffer, 1876, Monog. helic. viv., **7**, p. 361; Hidalgo, 1893, Obras Malac., **3**, pp. 80, 175–176.

Helix (*Isomeria*) *juno* Pfeiffer, von Martens, 1860, Die Heliceen, 2nd ed., p. 156; Pilsbry, 1889, Man. Conch. (2), **5**, pp. 152–153, pl. 45, figs. 13–14; Germain, 1907, Bull. Mus. National hist. nat., Paris, **13**, p. 54—Mindo, Ecuador (Rivet!); Germain, 1910, Miss. Arc de Méridien équatorial, **9**, pp. C.15–C.16.

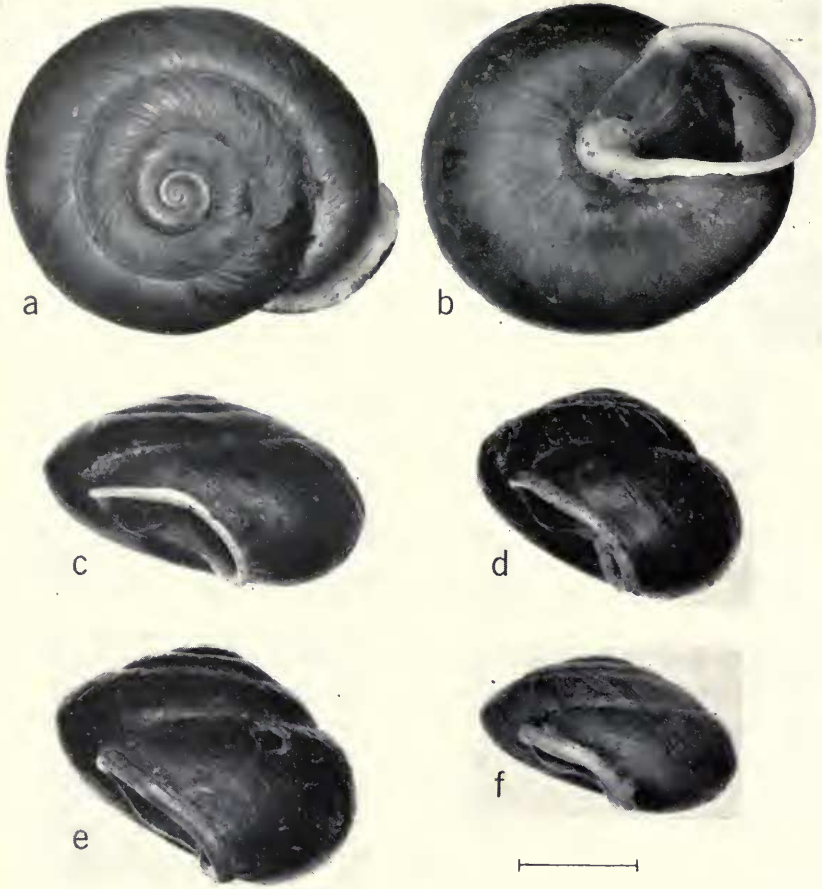


FIG. 41. Shells of: *a–c, Isomeria neogranadensis*, "New Granada." Zurich. Probably a paratype (*a*, top; *b*, base; *c*, side); *d, Isomeria bituberculata*, Baños, Tungurahua, Ecuador, CNHM 117842; *e, Isomeria juno*, Mera, Ecuador, CNHM 86650; *f, Isomeria hartwegi*, La Galia, Yaguachi, Ecuador, CNHM 40647. Scale line equals 10 mm.

Isomeria juno (Pfeiffer), Miller, 1878, Malak. Blätt., **25**, p. 171—Val de Pilatón, Ecuador (Boetzkes!); Cousin, 1887, Bull. Soc. Zool. France, **12**, pp. 256–257—Est. Pegado, Baeza, Napo, Ecuador (Cousin!).

Pleurodonte (*Isomeria*) *juno* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Ecuador: Recorded localities are—Napo, Nachiyacu and Baeza on the Río Napo; Puyo and Mera on the Río Pastaza; Mindo, Nanegal, Val de Pilatón on tributaries of the Río Guallabamba. No specimens have altitudinal data with them.

Material.—*Ecuador* (Edinburgh): Mera (CNHM 88650, Jackson 6998); Baeza (USNM 608877, SMF 82549); Nanegal (ANSP); Nachiyacu (Jackson 5104, ANSP 170706); Puyo (Jackson 6997, ANSP 170728); Oriente Prov. (CNHM 72338, CNHM 72349, USNM 628798); "Quito" (CNHM 95575, CNHM 102397, Zurich).

Diagnosis.—Basal lip with two inconspicuous swellings near the umbilicus, visible in subadults as distinct teeth; upper palatal lip usually with low swelling; umbilicus completely closed; umbilical callus and lip grossly thickened internally, obscuring teeth; periphery obtusely angulated with lighter color band; parietal callus with thick edge; surface with rather noticeable malleations and grooves. Diameter 28.1–35.8 mm. (mean 32.5 mm.), H/D ratio 0.513–0.657 (mean 0.600).

Remarks.—This can obviously be derived from *I. bituberculata*, differing in the more angulated periphery, with lighter color band,

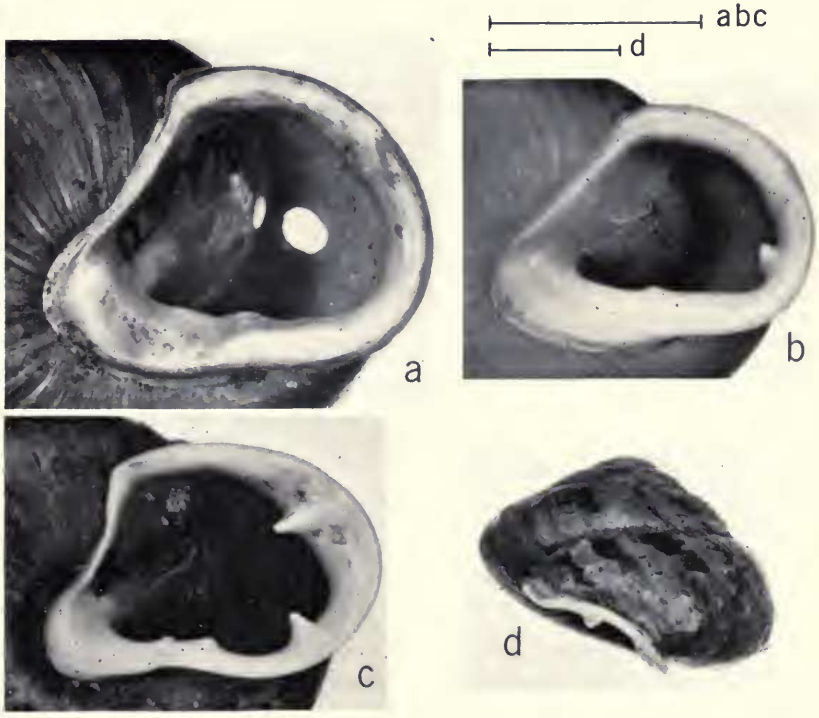


FIG. 42. Shells of: *a*, *Isomeria juno*, Mera, Ecuador, CNHM 86650. Aperture; *b*, *Isomeria hartwegi*, La Galia, Yaguachi, Ecuador, CNHM 40647. Aperture; *c–d*, *Isomeria bourcieri*, Mindo, Ecuador, CNHM 117847 (*c*, aperture; *d*, side). Scale lines equal 10 mm.

greatly thickened shell and lip, and the umbilical callus that reduces the prominence of the teeth. Most specimens show only the faintest trace of the upper palatal tooth and the basal teeth are reduced to low swellings.

No data is available on the ecological relationship of *juno* and *bituberculata*. Both have been reported from the same locality, although they were not collected at the same time. Apparently *I. juno* lives on both the Amazonian and Pacific slopes of the Ecuadorean Andes. No data is available as to its altitudinal range. The larger size, much thicker and heavier shell and absence of a lower palatal tooth separate *I. juno* from *I. hartwegi*. In older collections, *I. aequatoria* has been confused with *I. juno*. The former has a lower palatal tooth, lacks any surface malleations, and is generally larger in size.

Size and shape variation is within rather narrow limits, the ranges in diameter and obesity index being much less than in *I. bourcieri* or *I. bituberculata*.

Size variation in four localized sets is summarized in Table XIII. Plotting of the diameter and obesity index for all available specimens showed only slightly skewed distributions.

	Diameter in mm.							
	28.5		30.5	31.5	32.5	33.5	34.5	35.5
No. of specimens	1	1	4	12	13	19	2	2

	H/D ratio					
	0.515	0.545	0.575	0.605	0.635	0.665
No. of specimens	1	2	19	17	11	4

Isomeria bourcieri (Pfeiffer, 1853). Figure 42c–d.

Helix bituberculata Reeve, 1852 (not Pfeiffer, 1853), Conch. Icon., *Helix*, pl. 99, fig. 544—Tungaragua (=Tungurahua) (error), Ecuador (Bourcier!) (issued in May, 1852).

Helix bourcieri Pfeiffer, 1853, Monog. helic. viv., **3**, p. 209; Pfeiffer, 1854, Proc. Zool. Soc. London, **1852**, p. 153—Otoralo (=Otovalo), Ecuador (issued June 27, 1854); Pfeiffer, 1854, Syst. Conch. Cab., I (12), **3**, pp. 368–369, pl. 139, figs. 12–13 (plate issued in 1852); Pfeiffer, 1859, Monog. helic. viv., **4**, p. 243; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 315; Hidalgo, 1870, Moluscos del Viaje al Pacifico, pp. 15–16—Nanegal, Ecuador (Martinez!); Pfeiffer, 1876, Monog. helic. viv., **7**, p. 362; Hidalgo, 1893, Obras Malac., **3**, pp. 80, 178.

Helix (*Isomeria*) *bourcieri* Pfeiffer, von Martens, 1860, Die Heliceen, 2nd ed., p. 156; von Martens, 1885, Conch. Mitteil., **2** (5–6), p. 157—Nanegal, Ecuador (Stübel!); Pilsbry, 1889, Man. Conch. (2), **5**, p. 156, pl. 48, figs. 49–51; Reibisch, 1896, Abhl. Naturwiss. Gesell. Isis, Dresden, **7**, p. 55—

Nanegal, Ecuador; Germain, 1907, Bull. Mus. National hist. nat., Paris, **13**, p. 54—Nanegal, Rio Guallabamba, Ecuador (Rivet!).

Dentellaria bourcieri (Pfeiffer), Miller, 1878, Malak. Blätt., **25**, p. 166—Nanegal, Ecuador (Wolf!).

Isomeria bourcieri (Pfeiffer), Cousin, 1887, Bull. Soc. Zool. France, **12**, pp. 254–255—Los Puentes, near Gualea, Ecuador (Cousin!). Notes on ecology and color of animal.

Pleurodonte (*Isomeria*) *bourcieri* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Helix (*Isomeria*) *bituberculata* (Reeve), Germain, 1910, Miss. Arc de Méridien équatorial, **9** (3), pp. C.16–C.18.

Range.—Central Ecuador in the Upper Esmeraldas, Napo and Pastaza drainages. Recorded localities are: Mindo, Gualea, Sigchos, Mt. Pichincha, Milpe and Nanegal on tributaries of the Rio Guallabamba; Mera and Puyo on the upper Río Pastaza; Napo and Topo on the upper Río Napo; and Otovalo.

Material.—Ecuador (CNHM 247, CNHM 40648, CNHM 95578): Puyo, Rio Pastaza (CNHM 86668, ANSP 170725, Jackson 9338); Mindo (CNHM 117847, Jackson 4724); Sigchos, west of Latacunga (Jackson 9726); Mera (Jackson 5527); Milpe (Jackson 4821); Napo (Jackson 5290); Topo (Jackson 9988); Antisana (Jackson 10148); Tandayapa, west slope of Mt. Pichincha at 2,500 meters elevation (Jackson 11155, SMF 156320); Mt. Pichincha (Edinburgh); "Quito" (CNHM 50890, CNHM 102396, Zurich, Edinburgh).

Diagnosis.—Basal lip with two small, close-set, pointed teeth, occasionally with accessory denticles between; lower palatal lip with single small crescentic tooth; upper palatal lip with larger spade-like tooth and marked indention behind the lip; umbilicus closed; surface nearly smooth with weak growth lines; periphery obtusely angulated to rounded; parietal callus very thin, occasionally with raised edge; lip white; color reddish-brown with an irregular pattern of yellow markings. Diameter 21.2–32.2 mm. (mean 26.0 mm.), H/D ratio 0.562–0.715 (mean 0.636).

Remarks.—The color pattern is the same found in *Labyrinthus magdalenensis* and immediately separates *bourcieri* from the other *Isomeria*. The position of the basal teeth and form of the lower palatal tooth relate *bourcieri* to other members of this group. The very elevated spire, strong upper palatal tooth and color, I consider to be secondary modifications.

Most authors have called attention to Reeve's (*loc. cit.*) mislabeled figures, but only Germain in 1910 attempted to follow Reeve rather

than considering them an obvious error. Reeve cited the *Proceedings of the Zoological Society of London, 1852*, and listed Pfeiffer as the author of the species. It is clear that he intended to follow Pfeiffer's usage. The 1852 volume of the *PZSL* did not appear until 1854, giving Reeve's usage technical priority. Despite this, I have chosen to maintain the names in their Pfeifferean sense, since this will contribute to stability of nomenclature.

Most of the available specimens were inadequately localized, and the few sets with good data contained only three or four specimens. Most of these were remnants of larger sets after material had been traded to other museums or collectors. The result is that no statistical treatment of the data was thought justified. Plotting of the diameter distribution revealed the following quite skewed distribution, although the obesity index is much less distorted. The greater number of small shells may reflect the results of trading by collectors rather than the situation in natural populations. Only two specimens (Jackson 11155, SMF 156320) were accompanied by data on elevation (8,200 feet).

	Diameter in mm.					
	22.0	24.0	26.0	28.0	30.0	32.0
No. of specimens	8	13	15	24	2	2
	H/D ratio					
	0.560	0.590	0.620	0.650	0.680	0.710
No. of specimens	2	9	20	22	7	4

Isomeria hartwegi (Pfeiffer, 1846). Figures 41f, 42b.

Helix hartwegi Pfeiffer, 1846, Proc. Zool. Soc. London, **1845**, pp. 126–127—El Catamaija, near Loxa, Ecuador (Hartweg!); Pfeiffer, 1848, Monog. helic. viv., **1**, pp. 403–404; Reeve, 1852, Conch. Icon., *Helix*, pl. 104, fig. 575a–b; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 464; Dohrn, 1880, Jahrb. d. Malak. Gesell., **7**, p. 86—Synonymizes *loxensis* and *hartwegi*.

Isomeria hartwegi (Pfeiffer), Miller, 1878, Malak. Blätt., **25**, p. 171; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 256.

Isomeria loxensis (Miller), 1879, Malak. Blätt., n.f., **1**, p. 118, pl. 12, fig. 1—Catamayo Valley, Loja Prov., Ecuador at 3,000 feet elevation (Wolf!); Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 257.

Helix (*Isomeria*) *hartwegi* (Pfeiffer), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 153–154, pl. 45, figs. 15–16, pl. 64, fig. 26; Kobelt, 1893, Syst. Conch. Cab., I (12), **4**, pp. 631–632, pl. 181, figs. 7–9 (plate issued in 1886).

Pleurodonte (*Isomeria*) *hartwegi* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Helix (*Isomeria*) *loxensis* (Miller), Reibisch, 1896, Abhl. naturwiss. Gesell. Isis, Dresden, **7**, pp. 55–56—Cerritos de Taura, Guayaquil, Ecuador (Wolf!).

Range.—Southern Ecuador from Loja at 3,000 feet elevation north to Cuenca (8,400 feet elevation) and west to Taura and Yaguachi near Guayaquil.

Material.—Ecuador (Edinburgh, Zurich, ANSP 45557, ANSP 63579): La Galia, Yaguachi (CNHM 40647); Cuenca (CNHM 40646); "Toza, 7,000." (Zurich ex Mousson, G. Wallis 1877).

Diagnosis.—Basal lip with one or more very indistinct teeth or swellings; lower palatal lip with small conical tooth (occasionally absent); occasionally a peripheral notch results in a small swelling on the upper palatal lip; umbilicus rarely partly opened, usually closed; periphery nearly right angled; parietal callus with raised edge; surface with fine grooves, but no malleations. Diameter 23–27 mm. (mean 25.9 mm.), H/D ratio 0.479–0.574 (mean 0.511).

Remarks.—Pilsbry's copies (1889) of the type figures of *hartwegi* are very poor and totally misleading as to the form of the teeth and the color of the shell. It was probably these figures that led Reibisch (*loc. cit.*) to separate *hartwegi* and *loxensis*. The latter seems to be a slightly umbilicated form with well-developed basal teeth. In all of the specimens seen, the umbilicus was completely closed and the basal teeth represented by very vague bumps or at most weak knobs. In one example from "Toza" the lower palatal tooth was absent and in the single example from Cuenca it was greatly reduced.

The lower palatal tooth and more strongly carinated periphery easily separate *I. hartwegi* from the Colombian *I. basidens* and *I. neogranadensis*. The larger, much heavier shell of *I. juno* also lacks the lower palatal tooth.

The location of "Toza" is unknown and the position of "La Galia, Yaguachi" is uncertain since either the river near Guayaquil or the river near Zaruma could be correct.

Group of *Isomeria subelliptica*

The species agree in having a relatively widely open umbilicus for *Isomeria*, are generally of medium size (29–38 mm. in diameter)—although *I. continua* reaches nearly 50 mm. in maximum diameter and *I. minuta* is only 18.2 mm.—and have very reduced, simple dentition. Two of the species, *I. morula* and *I. aloagana*, are only known from their type collections and were not seen during this study; *I. anodonta* and *I. minuta* are known from single specimens; *I. subelliptica* from three specimens; and only *I. continua* is represented in museum collections by more than a dozen individuals. *I. morula* may be an

extreme variant of *I. bituberculata*, but the other species seem well characterized.

Isomeria anodonta from Cajamarca, Peru at 6,000 feet elevation lacks any trace of apertural teeth and has a raised spire with obtusely angulated periphery. *I. morula* has a basal and an upper palatal tooth, probably a flatly rounded spire and scarcely any angulation to the periphery. *I. aloagana* from the Pacific slopes of Central Ecuador apparently has two weak basal tubercles, a moderately elevated spire and an acutely angulated periphery. *I. continua* from the Magdalena drainage in Caldas east to Villavicencio in Meta, Colombia at 3,400–4,400 feet elevation has no basal or palatal teeth, but usually a small parietal lamella, a normally elevated spire and an acutely angulated periphery. Its probable replacement in the Cauca drainage at 3,600–4,000 feet elevation (so far known only from Valle de Cauca), *I. subelliptica*, has a small parietal lamella, a flatly rounded spire and a very obtusely angulated periphery. *I. minuta* has a lower palatal tooth, a basal tooth and an acutely angulated periphery, and probably lives in the same area as *I. continua*. A provisional key to the species follows.

KEY TO THE *ISOMERIA SUBELLIPTICA* GROUP

1. No lower palatal tooth 2
   A prominent lower palatal tooth ..... *Isomeria minuta* new species
2. Periphery of body whorl acutely angulated 3
   Periphery of body whorl obtusely angulated 4
3. Basal lip with small tubercles; Pacific Ecuador.
   Isomeria aloagana (Jousseaume, 1887)
   Basal lip without trace of teeth, often a small parietal lamella; Central Colombia ..... *Isomeria continua* (Pfeiffer, 1854)
4. No basal or palatal teeth present 5
   One basal and one upper palatal tooth ..... *Isomeria morula* (Hidalgo, 1870)
5. No parietal tooth; Peru ..... *Isomeria anodonta* Pilsbry, 1949
   Small parietal lamella present; Cauca drainage, Colombia.
   Isomeria subelliptica (Mousson, 1869)

Isomeria morula (Hidalgo, 1870)

Helix martinii Bernardi, 1858 (not Pfeiffer, 1854), Jour. de Conchyl., **7**, pp. 93–94, pl. 1, fig. 3—Quito, Ecuador; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 382; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 442.

Helix morula Hidalgo, 1870, Jour. de Conchyl., **18**, p. 32—new name for *Helix martinii* Bernardi, 1858, not *Helix martini* Pfeiffer, 1854.

Isomeria martinii (Bernardi), Miller, 1878, Malak. Blätt., **25**, p. 171.

Isomeria morula (Hidalgo), Cousin, 1887, Bull. Soc. Zool. France, **12**, pp. 257–258.

Helix (*Isomeria*) *martinii* Bernardi, Pilsbry, 1889, Man. Conch. (2), **5**, p. 149, pl. 45, fig. 20.

Pleurodonte (*Labyrinthus*) *martinii* (Bernardi), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Diagnosis.—Basal lip with single prominent tooth; upper palatal lip with moderately prominent denticle; umbilicus widely open; parietal callus with thick, raised edge; periphery obtusely angulated; surface granulated with malleations on body whorl; lip white. Diameter 32 mm. (adapted from the original illustration and description).

Remarks.—Under Article 58, Section 10 of the International Code of Zoological Nomenclature, the names *Helix martini* Pfeiffer, 1854, and *H. martinii* Bernardi, 1858, are homonyms and Hidalgo's substitute name must be used for the species, even though the Sumatran *Elaphroconcha martini* (Pfeiffer, 1854) belongs to a different family. During a brief study trip to Madrid, I was unable to locate any material of this species. The only specimens labeled as *I. morula* were misidentified *I. bituberculata*. Possibly, *I. morula* is a widely umbilicated variety of *bituberculata*, but until specimens can be examined, its status will remain uncertain.

Isomeria anodonta Pilsbry, 1949. Figure 44a–b.

Isomeria anodonta Pilsbry, 1949, Nautilus, **62**, (3), p. 100, pl. 6, figs. 3,a—Chaupo, Prov. Jaén, Dept. Cajamarca, Peru at 6,000 feet elevation (Carriker!).

Range.—Known only from the type locality.

Material.—Peru: CAJAMARCA—Chaupo, Prov. Jaén (ANSP 165202, holotype).

Diagnosis.—No apertural teeth; umbilicus widely open, contained 8.9 times in the diameter; periphery obtusely angulated; parietal callus with broad raised edge; surface with prominent radial growth striae, malleated on body whorl; lip brown. Diameter 39.2 mm., H/D ratio 0.517, with 4⅞ whorls.

Remarks.—The elevated spire and lack of dentition immediately separate *anodonta* from the other openly umbilicated forms. Only the holotype, a rather worn, dead specimen, is known. Of the other Peruvian species, *I. meobambensis* has a closed umbilicus and a large lower palatal tooth, while in *I. stoltzmanni* the umbilicus is partly closed, the periphery acutely angulated, and there is distinct palatal dentition.

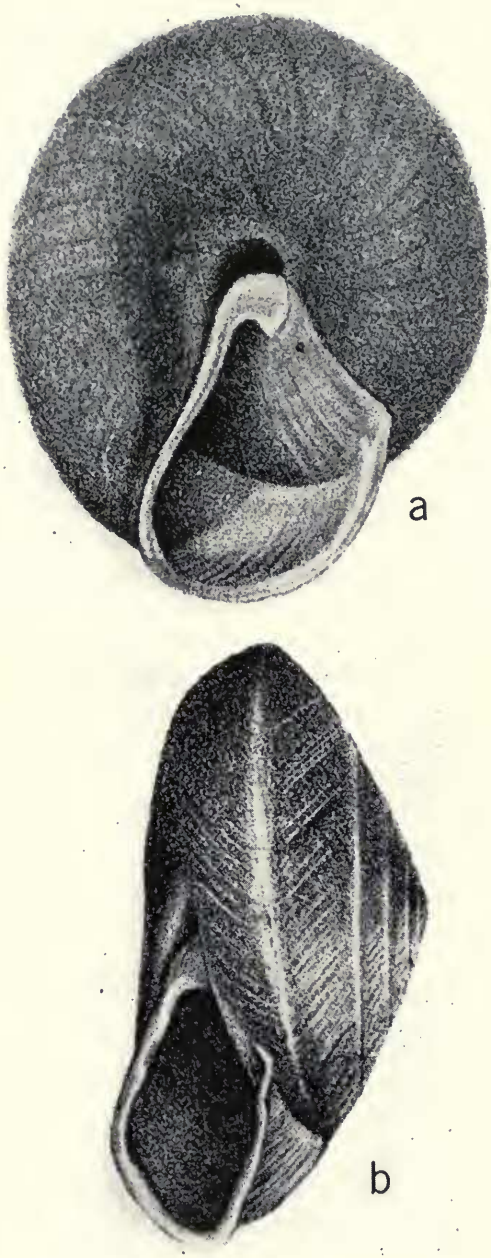


FIG. 43. *Isomeria aloagana*. Copied from *Bull. Soc. Zool. France*, **12**, pl. 3, figs. 6, 7 (1887). *a*, base; *b*, side.

Isomeria aloagana Jouseaume, 1887. Figure 43a–b.

Isomeria aloagana Jousseaume, 1887, Bull. Soc. Zool. France, **12**, pp. 179–180, pl. 3, figs. 6–7—trail from Aloag to Rio Toachi, Canton of Megia, Prov. Pichincha, Ecuador (Cousin!); Cousin, 1887, *op. cit.*, **12**, p. 254.

Helix (*Isomeria*) *aloagana* (Jousseaume), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 139–140, pl. 43, figs. 48–49.

Pleurodonte (*Isomeria*) *aloagana* (Jousseaume), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Diagnosis.—Basal lip with two inconspicuous tubercles; no parietal or palatal teeth; umbilicus partly covered by reflection of lip; periphery right angled; parietal callus very thin, without raised edges; surface minutely granulated with fine, radial growth lines. Diameter 35–38 mm., height 16–17 mm. (modified from original description).

Remarks.—The absence of any parietal and palatal teeth and the presence of two small basal tubercles are the main identifying features. Conceivably, this species is based on young individuals of a dwarf race of *Isomeria kolbergi* or possibly of *I. jacksoni*. The presence of fine granulations is much more characteristic of the *oreas* group.

No specimens could be located. The types are not in the Jousseaume collection in Paris. Birds from Aloag were taken from 7,800–9,570 feet, but where the specimens of *I. aloagana* came from is unknown. Probably they were taken somewhere in the upper Pilatón or Quitasol valleys.

Isomeria continua (Pfeiffer, 1854). Figure 44c–d.

Helix continua Pfeiffer, 1854 (June), *in* Reeve's Conch. Icon., *Helix*, pl. 184, fig. 1270—Province of Ocaña, Colombia (Schlim!); Pfeiffer, 1854 (November), Proc. Zool. Soc. London, **1853**, p. 128; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 308; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 464.

Helix (*Isomeria*) *continua* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 137, pl. 46, fig. 27.

Helix (*Isomeria*) *peritropis* Pilsbry, 1889, Man. Conch. (2), **5**, pp. 140–141, pl. 63, figs. 10–13—Bogotá, Colombia.

Pleurodonte (*Isomeria*) *peritropis* (Pilsbry), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Pleurodonte (*Isomeria*) *continua* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Isomeria continua (Pfeiffer), Pilsbry, 1935, Proc. Acad. Nat. Sci., Philadelphia, **87**, p. 83—region of Villavicencio, Colombia (Apolinar Maria!).

Range.—Central Colombia between Manizares, Caldas and Villavicencio, Meta. Described from "Province of Ocaña."

Material.—Colombia: "Bogotá (Edinburgh, SMF 172167, ANSP, ANSP 63585, ANSP 45555, ANSP 33134 types of *peritropis* Pilsbry). CALDAS—Manzanares at 1,340 meters (MCZ 145206). META-CUNDINAMARCA—Guayabetal at 1,030 meters (MCZ 143365);

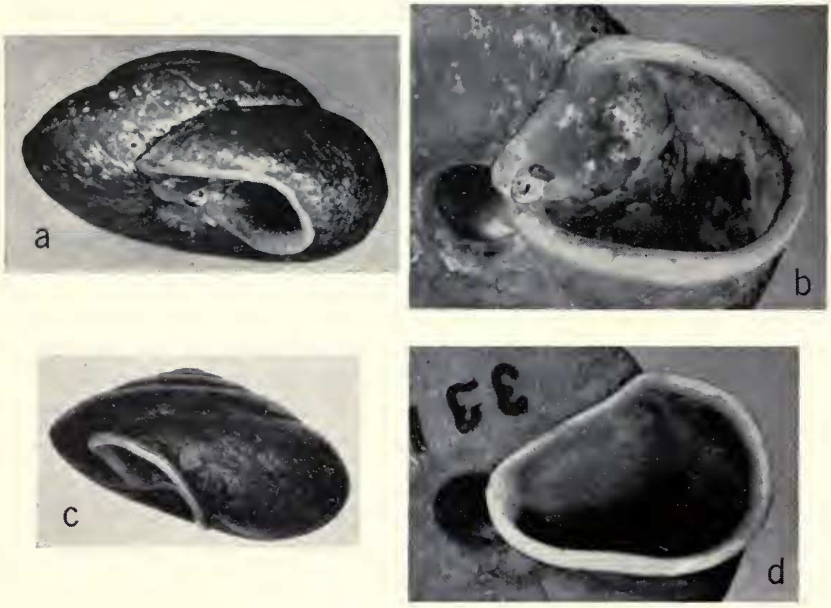


FIG. 44. Shells of: *a–b, Isomeria anodonta,* Chaupo, Jaén, Peru, ANSP 165202. Holotype (*a,* side; *b,* aperture); *c, Isomeria continua,* Bogotá, Colombia. Edinburgh; *d, Isomeria continua,* Bogotá, Colombia, ANSP 33134. Holotype of *peritropis* Pilsbry, 1889.

Pipiral on road from Bogotá to Villavicencio (Jackson 6105); region of Villavicencio (ANSP 164559).

Diagnosis.—Basal and palatal lip without dentition; parietal wall often with small ovate denticle; umbilicus widely open; periphery acutely angulated; spire normally elevated; lip white; parietal callus with narrow, strongly raised edge; surface with very weak, fine, growth lines. Diameter 29.6–49.7 mm. (mean 36.2 mm.), H/D ratio 0.433–0.523 (mean 0.471).

Remarks.—Apparently this is either highly variable in size, or two species are being confused. The type of *continua* (diameter 40.2 mm.), and three shells from "Bogotá" (Edinburgh, SMF 172167, ANSP 45555) (diameters 43.6, 43.5 and 49.7 mm., respectively) are very

large. Another specimen from "Bogotá" is 39.9 mm. in diameter. The other specimens range from 29.6–35.6 mm. in diameter, including the types of *peritropis*. The data accompanying the few localized shells gives no indication of the ecological conditions and the larger shells are not known from an exact locality.

The parietal tooth is present in nine of the ten small and none of the four large specimens examined, although found in the type of *continua*.

Only two localities included altitudinal data. The range of 3,375–4,390 feet is one of the lowest known for *Isomeria*.

Isomeria minuta new species. Figure 45a–d.

Diagnosis.—The smallest known species of *Isomeria*, diameter 18.2 mm., with broadly open umbilicus (D/U ratio 5.7), acutely angulated periphery, elevated spire, one large basal tooth and a single crescentic lower palatal tooth with posterior indention. The open umbilicus, shell form, parietal lip and sculpture relate this to the *I. subelliptica* complex, but the presence of a lower palatal tooth with posterior indention and a large basal tooth at once separate it as a distinct species.

Holotype.—Senckenberg Museum, Frankfurt-am-Main number 172174. Sierra de Mariquita at 2,170 meters elevation. Probably this is a portion of the Cordillera Central of the Andes near the Caldas–Tolima border above the town of Mariquita, Tolima, Colombia.

Description.—Shell very small, with 4¾ normally coiled whorls. Spire markedly and evenly elevated, apex protruding, sides of spire with faintly concave outline, although individual whorls distinctly rounded, H/D ratio 0.489. Apex and early spire somewhat worn, without distinctive sculpture, lower spire with prominent growth wrinkles and minute scattered granulations. Periphery acutely angulated, rounded on edge, flattened immediately above and below angulation. Color light greenish-yellow-brown with lighter flecks and streaks. Lip white. Umbilicus widely open, very slightly narrowed by expansion of parietal and basal lips, contained 5.7 times in the diameter, margins rounded. Aperture subquadrangular, moderately deflected, inclined about 50° from shell axis. Parietal wall with narrow, nearly straight, elevated callus lip, but no dentition. Basal-parietal margin sinuated, with basal lip nearly straight and a broad, high, rounded knob marking the outer edge. Lower palatal lip with single crescentic lamella marked by a weak posterior indention

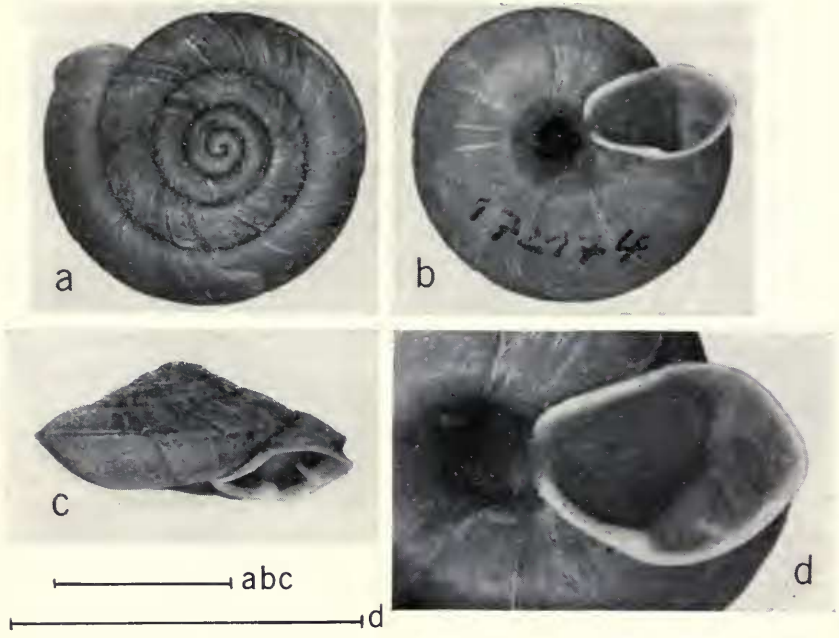


FIG. 45. *Isomeria minuta:* Sierra de Mariquita, Colombia, SMF 172174. Holotype. *a*, top; *b*, base; *c*, side; *d*, aperture. Scale lines equal 10 mm.

and a slight lateral buttress extending up to periphery. Peripheral lip distinctly angulated, lower portion of upper palatal lip straight, upper part curved. Lower palatal and basal lips moderately to strongly reflected, upper palatal lip only slightly reflected. Height of holotype 8.9 mm., diameter 18.2 mm.

Remarks.—The only data accompanying the single shell was "S. de Mariquita, 2170 m." The town of Mariquita, Tolima lies 17 km. west of Honda at the base of the Cordillera Central in the Magdalena drainage. Although the "Sierra de Mariquita" does not appear on any available map, this could be a local name or an early collector's attempt to designate a portion of the mountains above the town. Certainly this area would be the logical place to search for *I. minuta.*

As in the case of *I. inexpectata,* this species shows characters referable to both *Labyrinthus* and *Isomeria* and is thus described despite the availability of only a single example and the uncertain type locality. The large basal tooth at the outer edge of the basal lip and crescentic lower palatal tooth with posterior indention are typical of

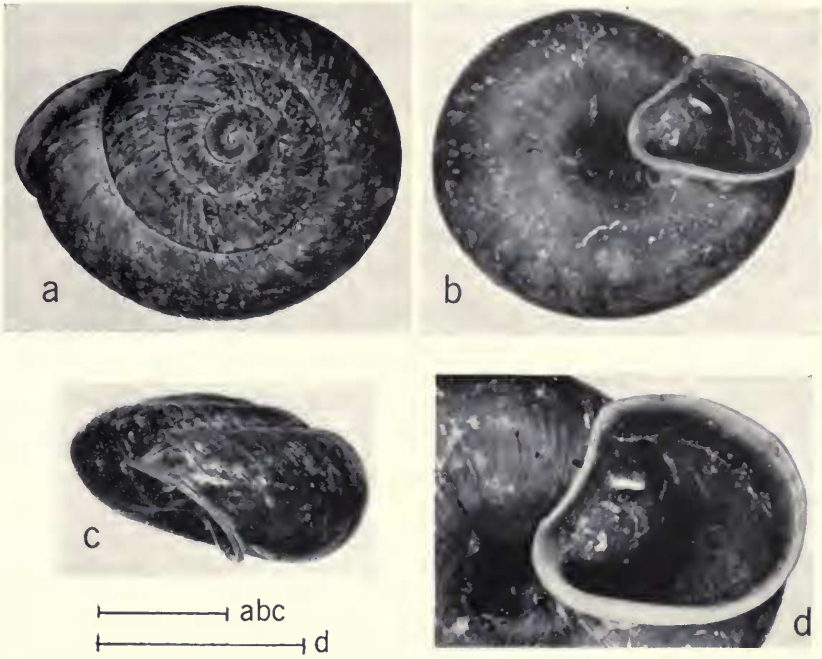


FIG. 46. *Isomeria subelliptica:* Bagua (=Buga), 4,000 feet elevation, Colombia. Zurich. Holotype. *a*, top; *b*, base; *c*, side; *d*, aperture. Scale lines equal 10 mm.

Labyrinthus and not seen in *Isomeria*, except for the large indented lower palatal tooth of *I. globosa*. The lack of any parietal dentition, the straight parietal lip (identical with that found in *I. continua*), the widely open umbilicus and sculpture of growth wrinkles and fine granulations are as in the *I. subelliptica* complex.

The probable geographic range lies within the range of *I. continua* and the altitude of 7,125 feet combines with the characters listed above to place *I. minuta* with the *I. subelliptica* complex rather than in *Labyrinthus*. The characters of *I. minuta* suggest that the transition from *Labyrinthus* to *Isomeria* (or vice versa) may have happened several times.

Isomeria subelliptica (Mousson, 1869). Figure 46a–d.

Helix subelliptica Mousson, 1869, Malak. Blätt., **16**, pp. 170–171—Bugua (=Buga?), Amazonas at 4,000 feet elevation (Wallis!); Pfeiffer, 1875, Novit. Conch., **4**, pp. 117–118, pl. 127, figs. 4–6; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 464.

Helix (*Isomeria*) *subelliptica* Mousson, Pilsbry, 1889, Man. Conch. (2), **5**, p. 139, pl. 46, figs. 28–30; Kobelt, 1894, Syst. Conch. Cab., I (12), **4**, p. 628, pl. 180, figs. 8–11.

Pleurodonte (*Isomeria*) *subelliptica* (Mousson), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Cauca River Valley in Valle de Cauca, Colombia.

Material.—*Colombia:* "Ocanna" (Zurich). VALLE DE CAUCA —gardens of Cali at 1,100 meters (USNM 251176); Buga (=Bugua) at 4,000 feet elevation (Zurich, holotype of *subelliptica*).

Diagnosis.—Basal and palatal lips without teeth; parietal wall with small crescentic lamella transversely situated above periphery; umbilicus widely open, lips covering only a small portion; periphery obtusely angulated, spire flatly rounded, lip brownish; parietal callus with narrow, sharply raised edge; surface with fine, crowded, growth striae. Diameter 29.0–34.6 mm. (mean 30.9 mm.), H/D ratio 0.456–0.575 (mean 0.507).

Remarks.—Through a curious typographical error, the major diameter has been recorded in the literature as 38 mm., although the minor diameter was listed correctly as 23 mm. Actual measurements of the holotype are—major diameter 29.2 mm. and minor diameter 23.2 mm. The small size, very wide umbilicus (D/U ratio 5.9–11.9) and obtusely angled periphery separate *subelliptica* from *I. continua* and *I. anodonta*. The single shell from Cali is atypical in having a narrower umbilicus, higher spire and thicker, much more strongly reflected lip. Both localized specimens were taken between 3,600 and 4,000 feet elevation.

Group of *Isomeria meobambensis*

The species are of medium size, diameter 30–42 mm., with totally closed umbilicus and a right-to-obtusely angulated periphery. They are known from Southern Ecuador and Peru. Usually only the surface has noticeable radial growth ribs, but *I. meyeri* and *I. gealei* show marked malleations near the periphery. *I. meyeri* completely lacks dentition. *I. gealei* and *I. aequatoria* agree in having a mid-basal, transversely situated lamella (larger in *aequatoria*), a prominent lower palatal tooth (very large and transversely twisted in *gealei*), and the upper palatal lip with a weak (*aequatoria*) to prominent (*gealei*) triangular knob forming the upper edge of a peripheral notch. *I. meobambensis* lacks basal and upper palatal dentition, having only a single lower palatal tooth with a lateral extension reaching the periphery (fig. 47b) that is unique in *Isomeria*.

The range of *I. meyeri* (Östlichen Cordillera von Ecuador) is unknown; *I. meobambensis* has been reported only from Moyobamba, San Martín, Peru; *I. gealei* from Malacatos, southern Ecuador; and *I. aequatoria* from the upper Chanchan drainage on the Pacific slopes of central Ecuador.

A key to the species follows.

KEY TO THE *ISOMERIA MEOBAMBENSIS* GROUP

1. Aperture with denticles.....2
   Aperture without denticles.....*Isomeria meyeri* (Strubell, 1894)
2. Basal tooth present; lower palatal tooth a simple or twisted lamella.....3
   Basal tooth absent; lower palatal tooth with upper lateral extension.
   Isomeria meobambensis (Pfeiffer, 1857)
3. Lip iridescent; basal tooth very small; body whorl with malleations.
   Isomeria gealei (E. A. Smith, 1877)
   Lip brown; basal tooth large; body whorl without malleations.
   Isomeria aequatoria (Pfeiffer, 1860)

Isomeria meobambensis (Pfeiffer, 1857). Figure 47a–b.

Helix meobambensis Pfeiffer, 1857, Proc. Zool. Soc. London, **1856**, p. 328—Moyobamba, Peru (Porte!); Pfeiffer, 1859, Monog. helic. viv., **4**, p. 243; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 361.

Helix (*Isomeria*) *meobambensis* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 144.

Pleurodonte (*Isomeria*) *meobambensis* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94; Haas, 1951, Fieldiana: Zool., **31** (46), pp. 511–512—Peru (type lot specimen of *I. anestia* Pilsbry, 1949).

Isomeria anestia Pilsbry, 1949, Nautilus, **62**, (3), pp. 99–100, pl. 6, figs. 4, 4a, 4b —probably Peru.

Labyrinthus (*Isomeria*) *meobambensis* (Pfeiffer), Weyrauch, 1964, Acta Zool. Lilloana, **20**, p. 60.

Range.—Known only from the type locality.

Material.—Peru (SMF 141090, CNHM 30704, type lot of *anestia* Pilsbry, 1949; CNHM 40640; ANSP 184497, types of *anestia* Pilsbry, 1949): SAN MARTÍN—Moyobamba (Zurich, Edinburgh ex Cuming, Brit. Mus., probably cotypes).

Diagnosis.—Basal lip straight, without teeth or swelling; lower palatal lip with a small conical tooth that has a high upper extension reaching periphery; umbilicus completely covered; periphery nearly right angled; parietal callus very thin, upper and lower edges slightly raised; surface with rather heavy radial ribs and grooves. Diameter 30.6–37.2 mm. (mean 34.3 mm.), H/D ratio 0.482–0.556 (mean 0.529).

Remarks.—Pfeiffer's species was never figured and its identification with *anestia* Pilsbry is based on material in older collections

labeled as *meobambensis*. They match the types of *anestia* and the description of *meobambensis* perfectly.

The peculiar lower palatal tooth with lateral extension that reaches the periphery through an extension is unique among *Isomeria*. When combined with the relatively strong radial sculpture, there is no species with which it can be confused. The presently unclassifiable *I. equestrata* Moricand, 1858 (see p. 194) may be based on a slightly subadult specimen of *I. meobambensis*.

Variation in part of the type set is summarized in Table XIII.

Isomeria gealei (Smith, 1877). Figure 47c–d.

Helix (Isomeria) gealei Smith, 1877, Proc. Zool. Soc. London, **1877**, pp. 361–362, pl. 39, fig. 9a, b—Malacatos, South Ecuador (Geale!); Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 255; Pilsbry, 1889, Man. Conch. (2), **5**, pp. 149–150, pl. 61, figs. 4–5.

Helix gealei Smith, Dohrn, 1886, Syst. Conch. Cab., I (12), **4**, pp. 626–627, pl. 180, figs. 5–6.

Isomeria gealei (Smith), Miller, 1879, Malak. Blätt., n.f., **1**, p. 193; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 255.

Pleurodonte (Isomeria) gealei (Miller), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Cordillera de Zamura, south of Loja, southern Ecuador.

Material.—Ecuador (CNHM 40644, USNM 125909, ANSP 33135, Zurich, Edinburgh): Malacatos (Jackson 7506); Toza, 7,000 feet elevation (Zurich, ex Mousson, Wallis, 1877).

Diagnosis.—Basal lip with one low diagonal tooth; lower palatal lip with high, brownish white, transversely twisted lamella bordering a deep peripheral notch; upper edge of peripheral notch protruded to form a small triangular knob; umbilicus completely covered; parietal callus thin with thickened, raised edge; periphery acutely angulated with protruding keel; surface with faint growth striae and grooves, moderately heavily malleated on body whorl; lip purplish tinted and iridescent. Diameter 33.5–41.2 mm. (mean 36.0 mm.), H/D ratio 0.505–0.557 (mean 0.531).

Remarks.—The purplish, iridescent lip with the white-tipped, transversely twisted lower palatal lamella immediately identifies this species. No other *Isomeria* can be confused with it. The upper palatal knob is very much like that in *Labyrinthus otostomus*.

Malacatos is on the slopes of the Cordillera de Zamura below Loja and the type specimens probably came from between 5,000 and 6,500 feet elevation. The location of Toza is unknown.

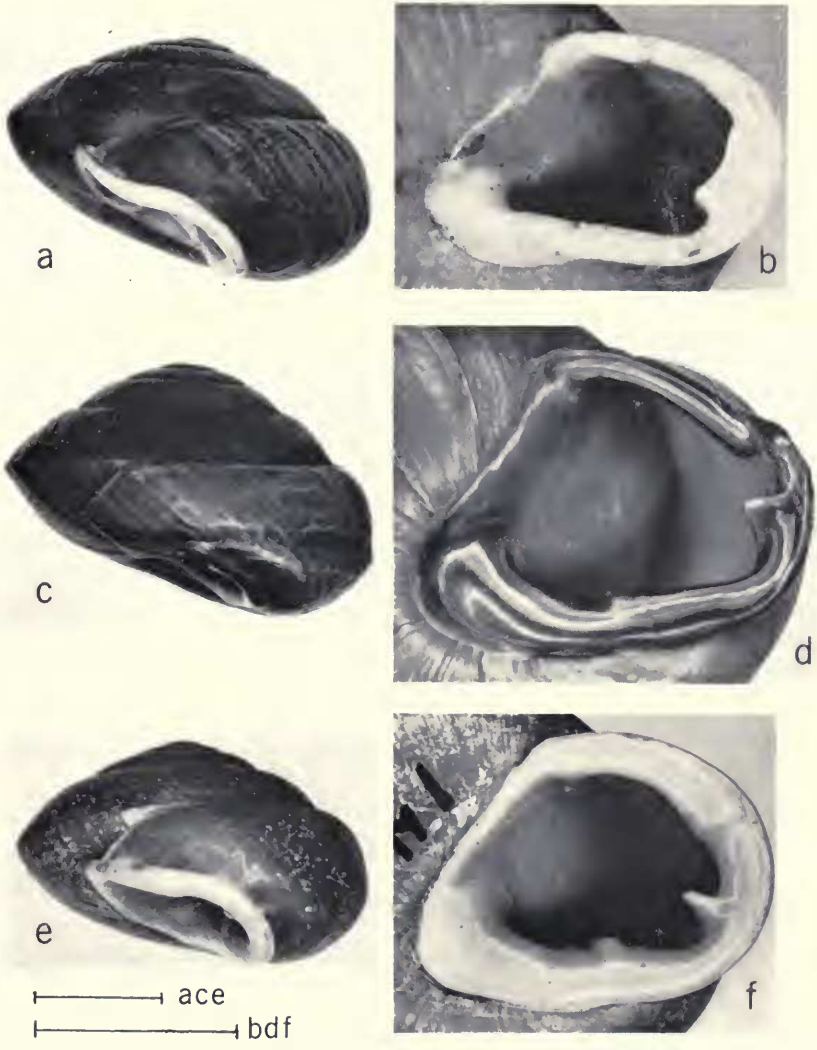


FIG. 47. Shells of: *a*, *Isomeria meobambensis*, Peru, CNHM 40640. Side; *b*, *Isomeria meobambensis*, Peru, ANSP 184497. Holotype of *anestia* Pilsbry, 1949. Aperture; *c–d*, *Isomeria gealei*, Ecuador, CNHM 40644 (*c*, side; *d*, aperture); *e–f*, *Isomeria aequatoria*, 6 miles below Huigra, Ecuador, ANSP 148483 (*e*, side; *f*, aperture). Scale lines equal 10 mm.

Isomeria aequatoria (Pfeiffer, 1860). Figure 47e–f.

Helix aequatoria Pfeiffer, 1860, Proc. Zool. Soc. London, **1860**, pp. 133–134, pl. 50, fig. 6—Ecuador (Fraser!); Pfeiffer, 1868, Monog. helic. viv., **5**, p. 314; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 361.

Isomeria aequatoria (Pfeiffer), Miller, 1878, Malak. Blätt., **25**, p. 170; Cousin, 1887, Bull. Soc. Zool. France, **12**, pp. 253–254.

Helix (*Isomeria*) *aequatoria* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 150–151, pl. 48, figs. 44–46; Kobelt, 1893, Syst. Conch. Cab., I (12), **4**, p. 629, pl. 180, figs. 12–13 (plate issued in 1886); Reibisch, 1896, Abhl. naturwiss. Gesell. Isis, Dresden, **7**, p. 55—Cayandelet, western Mts., Ecuador (Wolf!).

Pleurodonte (*Isomeria*) *aequatoria* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Central Ecuador in the upper Chanchan drainage. The only recorded localities are Huigra and Cayandeled.

Material.—Ecuador (CNHM 40638, ANSP 78358, MCZ, ZMA, Edinburgh, CNHM 132555): six miles below Huigra, Chanchan River (ANSP 148483); "Quito" (ANSP 30644, MCZ 88157, Zurich).

Diagnosis.—Basal lip with high conical, transversely slanted lamella; lower palatal lip with higher, narrower tooth; upper palatal lip with low triangular swelling just above periphery; umbilicus completely covered; periphery right or obtusely angled; lip tinged with brown; parietal callus thin with slightly raised edge; surface with fine growth lines and grooves. Diameter 32.0–39.8 mm. (mean 35.7 mm.), H/D ratio 0.556–0.609 (mean 0.590).

Remarks.—The form of the teeth is nearly identical to that of *I. gealei*, but the different color of the lip, transverse lower palatal tooth, malleated body whorl, and greater angulation of the latter, immediately separate the two species. *I. triodonta* could be confused with *I. aequatoria*, but the former has two basal teeth, a second palatal tooth, usually a partially open umbilicus and the body whorl shows distinct malleations.

The two known localities are both in the upper Chanchan drainage on the Pacific slopes. Ornithological collecting at these places ranged from 2,600–7,000 feet elevation. The altitudinal range of *I. aequatoria* is unknown.

Isomeria meyeri (Strubell, 1894)

Helix (*Isomeria*) *meyeri* Strubell, 1894, Syst. Conch. Cab., I (12), **4**, pp. 693–694, pl. 198, figs. 3–4—Östlichen Cordillera von Ecuador.

Diagnosis.—Aperture without teeth; umbilicus closed by basal and parietal lips which flatten into a broad callus; periphery right angled; surface heavily malleated; parietal callus thin; lip yellowish white. Diameter 36 mm., height 21 mm.

Remarks.—The heavy malleations on the shell and total lack of apertural teeth separate *I. meyeri* from other members of this group. The form of the basal lip is very similar to that found in *I. aequatoria*, hence its placement with this complex. No exact locality has been reported for this species and the type specimen could not be located. A slightly shortened translation of the detailed original description follows:

> Shell imperforate, compressed, transversely widened, solid, but not exceptionally thick; surface with transverse growth wrinkles and fine, somewhat wavy, microscopic spiral lines; color yellow-brown, with broad, wavy chestnut brown stripes that coalesce on base of shell. Spire flatly conical with smooth, rather pointed, whitish apex. Whorls four, sutures impressed and finely crenulated; upper whorls weakly rounded, slowly increasing in width, body whorl inflated, flattened for a short distance below the suture, shouldered, then rounded on base to the impressed umbilical callus. Aperture deflected, egg-shaped, bluish inside with a light peripheral zone. Lip white, thick, reflected, upper and basal margins almost parallel, outer margin abruptly rounded, basal margin elongated, ascending obliquely and forming a slightly curved, hardly widened blunt fold when covering the umbilicus. Parietal callus thin.

Recognition of this species should be quite easy, since the combination of no teeth, totally closed umbilicus and malleated shell is not matched by any other species of *Isomeria*.

Group of *Isomeria oreas*

Normally these are large shells (mean diameter over 39 mm.), whose combinations of characters vary so greatly that the group cannot be characterized concisely. The changes in each shell feature from species to species are small enough that no separation into species groups seems necessary, yet the total range of variation for all species is large enough that diagnostic separation from the *I. meobambensis* complex is difficult.

A series of alterations in form and structure can be traced between the larger and smaller types that cover most of the included species. Conceivably, as in *Labyrinthus*, it is most probable that changes from the smaller to the larger are the more logical assumption. For discussion purposes, however, either way of describing the changes is valid. I've chosen to start with the very large *I. oreas* and trace the pattern of changes then observed in the other, smaller species.

I. oreas has a large shell with very obtusely angled periphery, an open umbilicus with clearly visible internal groove, weak malleations

on the later whorls, and prominent parietal and basal teeth. In the slightly smaller *I. kolbergi* the umbilicus is distinctly narrower although the internal groove is still visible, the parietal tooth is missing, the malleations are more prominent and the periphery is more angulated. *I. triodonta* has an even narrower umbilicus, but possesses additional apertural teeth and heavier malleations with a sharper peripheral angulation. The small Peruvian *I. stoltzmanni* has a wider umbilicus than *kolbergi*, but lacks the malleations, is finely granulated and retains the lower palatal tooth. This is similar to *I. jacksoni*, which differs in having a nearly closed umbilicus and lacks both malleations and granulations. A slight alteration in pattern is seen in three species that have a secondary calcareous plate increasing the closure of the umbilicus. *I. cymatodes* has a parietal tooth, is very heavily malleated and has an obtusely rounded periphery. In Colombia, *I. scalena* with no apertural teeth and weak malleations, plus *I. fordiana* with only a weak lower palatal tooth and no malleations on the shell, have the same umbilical closure. This leaves two species that are rather distinctive. *I. aequatoriana* normally has the umbilicus closed by expansion of the basal and parietal lips and lacks all malleations, although very finely granulated on the surface. *I. globosa*, which extends into the coastal regions of Ecuador, has a narrow to closed umbilicus, a finely granulated surface and an extremely large lower palatal tooth with a marked posterior indention. The posterior indention is unique in *Isomeria*, although common in the *isodon* and *raimondii* series of *Labyrinthus*. Since *I. globosa* is the only truly lowland species of *Isomeria*, it is an intriguing possibility that the tooth structure is an attempt to narrow the aperture against predators found in lowland areas. Tooth development in *I. globosa* may parallel the tooth development in *Labyrinthus*.

Distributional data are sparse to abundant. Surprisingly, although 44 specimens of *I. triodonta* were found in museum collections, no locality is known for this species. *I. oreas* has a wide range in the Cauca and Magdalena drainages of Colombia. *I. scalena* is known only from the headwaters of the Rio Magdalena drainage and *I. fordiana* has been reported from Marmato and (dubiously) Ocaña. *I. stoltzmanni* in Cajamarca, Peru is the southernmost species of *Isomeria; I. globosa* ranges from southern Colombia to southern Ecuador in the Pacific drainage and has crossed over into the Upper Amazonian drainage; and *I. aequatoriana* is found only in the upper Amazonian areas. The remaining species, *I. cymatodes*, *I. kolbergi* and *I. jacksoni* have the same distribution, living in the Upper Rio Esmereldas drainage and Upper Amazonian drainage.

KEY TO THE *ISOMERIA OREAS* COMPLEX

1. Lower palatal tooth very small or absent, never marked by a deep posterior indention....2
   Lower palatal tooth very large, clearly marked by a deep posterior indention. *Isomeria globosa* (Broderip, 1832)
2. No parietal tooth present....4
   A distinct parietal tooth present....3
3. Umbilicus moderately open with columellar groove visible; surface with few weak malleations near periphery; Colombia....*Isomeria oreas* (Koch, 1844)
   Umbilicus nearly to completely closed by an accessory plate extending from lips; heavy malleations on body whorl; Ecuador. *Isomeria cymatodes* (Pfeiffer, 1852)
4. Lip with one or more teeth....5
   Lip without teeth....*Isomeria scalena* (von Martens, 1881)
5. Surface of body whorl moderately to heavily malleated; periphery acutely angled....6
   Surface of body whorl without malleations; periphery usually right or obtusely angled....7
6. Only lower palatal tooth present; umbilicus distinctly open; lip white. *Isomeria kolbergi* Miller, 1878 (Ecuador) OR *Isomeria fauna* (Philippi, 1851) (Colombia) (see p. 194)
   Basal, lower palatal and upper palatal teeth; umbilicus reduced to a slit or closed; lip with brown tints....*Isomeria triodonta* (Orbigny, 1835)
7. Umbilicus closed or a very narrow slit....8
   Umbilicus open, contained 12–14 times in the diameter; Peru. *Isomeria stoltzmanni* (Lubomirski, 1879)
8. Basal and parietal lips not expanded to form a callus completely closing umbilicus; diameter less than 46 mm....9
   Basal and parietal lips expanding to form a smooth callus that completely closes umbilicus (rarely leaving a microscopic lateral crack); diameter usually much more than 45 mm....*Isomeria aequatoriana* (Hidalgo, 1867)
9. Shell surface with microscopic granulations; Colombia. *Isomeria fordiana* (Pilsbry, 1889)
   Shell surface without such granulations; Ecuador. *Isomeria jacksoni* Solem, 1966

Isomeria oreas (Koch, 1844). Figures 48a–b, 49a.

Helix oreas Koch, 1844, *in* Philippi's Abbild. Besch. neuer Conchy., **1**, pp. 151–152, *Helix*, pl. 5, fig. 2—mountains of Colombia; Pfeiffer, 1848, Monog. helic. viv., **1**, pp. 400–401; Pfeiffer, 1851, Syst. Conch. Cab., I (12), **2**, pp. 55–56, pl. 75, figs. 1–3 (plate issued in 1849); Reeve, 1852, Conch. Icon., *Helix*, pl. 99, fig. 546; Pfeiffer, 1853, Monog. helic. viv., **3**, p. 257; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 308; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 412; Mousson, 1873, Malak. Blätt., **21**, p. 2; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 464.

Helix procera Pfeiffer, 1854 (June), *in* Reeve's Conch. Icon., *Helix*, pl. 184, fig. 1273—Antioquia, Colombia; Pfeiffer, 1854 (November), Proc. Zool. Soc. London, **1853**, p. 127; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 308; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 412; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 464.

Helix (*Isomeria*) *oreas* Koch, von Martens, 1885, Conch. Mitteil., **2** (5–6), p. 156—Ibagué, Colombia at 1,280 meters elevation (Stübel!); Pilsbry, 1889, Man. Conch. (2), **5**, pp. 136–137, pl. 45, figs. 11–12, 17–19, pl. 48, fig. 43; Dohrn, 1894, Syst. Conch. Cab., I (12), **4**, p. 627, pl. 180, fig. 7—monstrosity.

Pleurodonte (*Isomeria*) *oreas* (Koch), Pilsbry, 1894, Man. Conch. (2), **9**, pp. 93–94.

Isomeria oreas (Koch), Piaget, 1912, Mem. Soc. neuchateloise Sci. nat., **5**, p. 257—Angelópolis, near Titiribí, Prov. Antioquia, Colombia (Fuhrmann!); Pilsbry, 1935, Proc. Acad. Nat. Sci., Philadelphia, **87**, p. 83—Calarcá, Colombia (Apolinar Maria!).

Isomeria oreas var. *parvula* Piaget, 1912, *loc. cit.*, **5**, p. 257, pl. 9, fig. 8—Angelópolis, near Titiribí, Prov. Antioquia, Colombia at 1,970 meters elevation (Fuhrmann!).

Range.—Colombia, valley of the Río Cauca and Cordillera Central from Frontino or Angelópolis, Antioquia south to Popayán, Cauca. Also at Villavicencio, Meta. Recorded from 3,900–9,500 feet elevation.

Material.—Colombia (CNHM 245, CNHM 40636, ANSP 30641, USNM 307678, USNM 316112–316115, ZMA, Zurich): CALDAS—Salamina (Jackson 6305, USNM 518434); Mt. Quindiu (Paris); Marmato (ANSP 9272, ANSP 30642); Calarcá (ANSP 164560); Valle de Magdalena at 1,200 meters (MCZ 145205). ANTIOQUIA (Brit. Mus., types of *procera* Pfeiffer)—Támesis (Jackson 6311); ?Frontino (Zurich ex Wallis 1881). TOLIMA—Mt. Tolima (SMF). VALLE DE CAUCA—Río Paila Valley, 1,800 meters, Central Cordillera (USNM 251172). CAUCA (ANSP 91219, Edinburgh)—Río Palo headwaters, 2,900 meters, Central Cordillera (USNM 251174); Popayán (SMF); La Cumbre, near Popayán (ANSP 132448); Quilichao (Edinburgh). HUILA—Río Páez Valley, 2,900 meters, Central Cordillera (USNM 251173). CUNDINAMARCA—?Bogotá (Zurich ex Wallis 1872, Paris). META—?Sonora (Zurich); Caño Grande, Villavicencio (MCZ 146366). *"Ecuador"* (ANSP 63587, Zurich).

Diagnosis.—Parietal wall with small but prominent crescentic tooth; lower palatal lip with small conical tooth; periphery obtusely angulated; umbilicus widely open with noticeable columellar groove; surface with rather fine radial striae, weakly malleated near periphery; parietal callus thin or with prominent raised edge; lip white, edge brownish; color dull liver brown. Diameter 43.0–72.4 mm. (mean 57.3 mm.), H/D ratio 0.450–0.597 (mean 0.528).

Remarks.—Germain recorded *I. oreas* from Horongo, Nanegal and Cordillera de Intag in the upper Rio Esmereldas drainage of Ecuador, but his records are erroneous. The specimens are preserved in the

TABLE XIV—Size and shape variation in *Isomeria oreas*, *I. kolbergi* and *I. jacksoni*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
I. oreas													
MCZ 145205; Valle de Magdalena, Colombia	5	27.0	24.5–29.1	0.79	52.6	50.0–55.3	1.14	0.510	0.459–0.582	0.021	12.2	9.6–14.3	0.89
USNM 251174; Rio Palo, Colombia	4	30.4	26.8–32.0	1.22	54.8	52.1–57.3	1.08	0.555	0.514–0.585	0.013			
ANSP 91219; Cauca, Colombia	46	31.3	26.3–37.3	0.36	59.7	52.4–66.6	0.51	0.524	0.480–0.576	0.003	14.6	10.1–26.0	0.49
I. kolbergi													
Jackson 5517; Mera, Ecuador	37	24.8	21.2–30.0	0.31	49.4	42.8–55.4	0.58	0.502	0.445–0.572	0.005	22.1	14.3–36.5	0.89
Jackson 6226; Puyo, Ecuador	10	25.4	23.8–27.0	0.35	52.8	49.1–56.4	0.66	0.482	0.449–0.520	0.006	21.7	15.1–33.4	1.66
Jackson 7433; Topo, Ecuador	2	27.9	26.0–29.8	1.90	56.3	49.3–63.3	7.00	0.499	0.471–0.528	0.029	21.3	16.6–26.0	4.70
I. jacksoni													
Jackson 9364; Mera, Ecuador	5	18.7	17.2–20.7	0.57	35.6	32.2–41.5	1.69	0.527	0.499–0.554	0.010	21.6	18.4–24.6	1.27
Jackson 6820; Puyo, Ecuador	4	21.0	19.0–22.1	0.70	40.8	38.6–42.1	0.78	0.514	0.492–0.530	0.008	36.3	25.7–52.0	6.33
Jackson 10915; Topo Ecuador	3	22.8	22.3–23.9	0.53	45.0	44.8–45.4	0.18	0.507	0.496–0.526	0.010	16.8	15.1–19.4	1.31

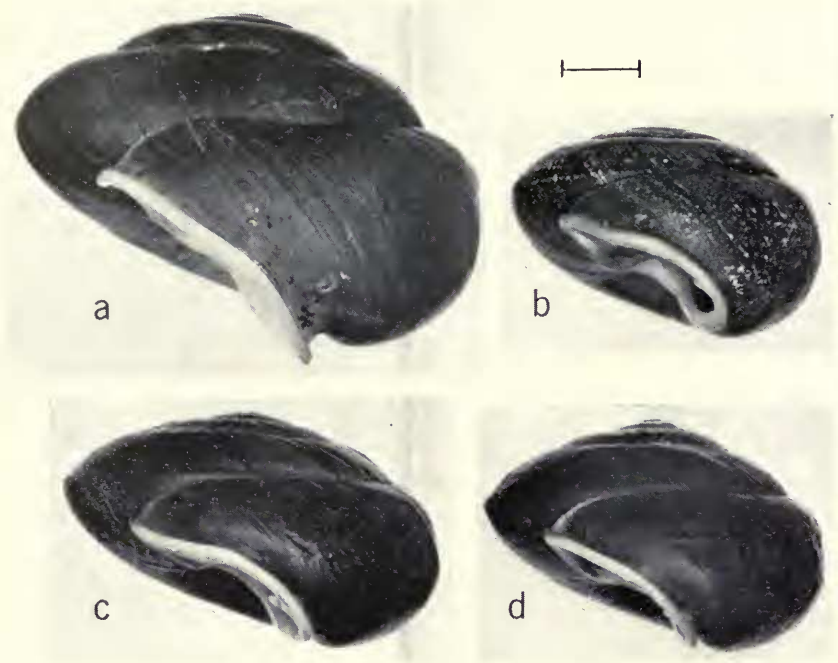


FIG. 48. Shells of: *a*, *Isomeria oreas*, "Ecuador." Zurich, large; *b*, *I. oreas*, Frontino, Antioquia, Colombia. Zurich, small; *c*, *Isomeria kolbergi*, Los Puentes, Ecuador, CNHM 117850; *d*, *Isomeria triodonta*, Ecuador, CNHM 40641. Scale line equals 10 mm.

Museum National d'Histoire Naturelle, Paris and are a mixture of two species—*I. kolbergi* and *I. cymatodes* (see below).

Most of the valid records are from the Cordillera Central of Colombia. Two records from the west side of the Cauca River, the material from Villavicencio, Dept. Meta and two questionable localities in the Mousson material (Sonora, Dept. Meta and Frontino, Dept. Antioquia) are the only exceptions. Six sets or literature records were accompanied by elevation data, ranging between 3,900–9,500 feet elevation. No obvious correlation between size and elevation could be seen, and only a tenuous correlation between size and locality. The specimens from Antioquia were less than 51 mm. in diameter, except for some from Angelópolis reported by Piaget (*loc. cit.*). The small specimens were called form *parvula* Piaget, 1912. Possibly this will be shown to be a valid geographic race, but too little material is currently available. Unfortunately, the only large set seen (ANSP 91219) was not specifically localized. Size variation

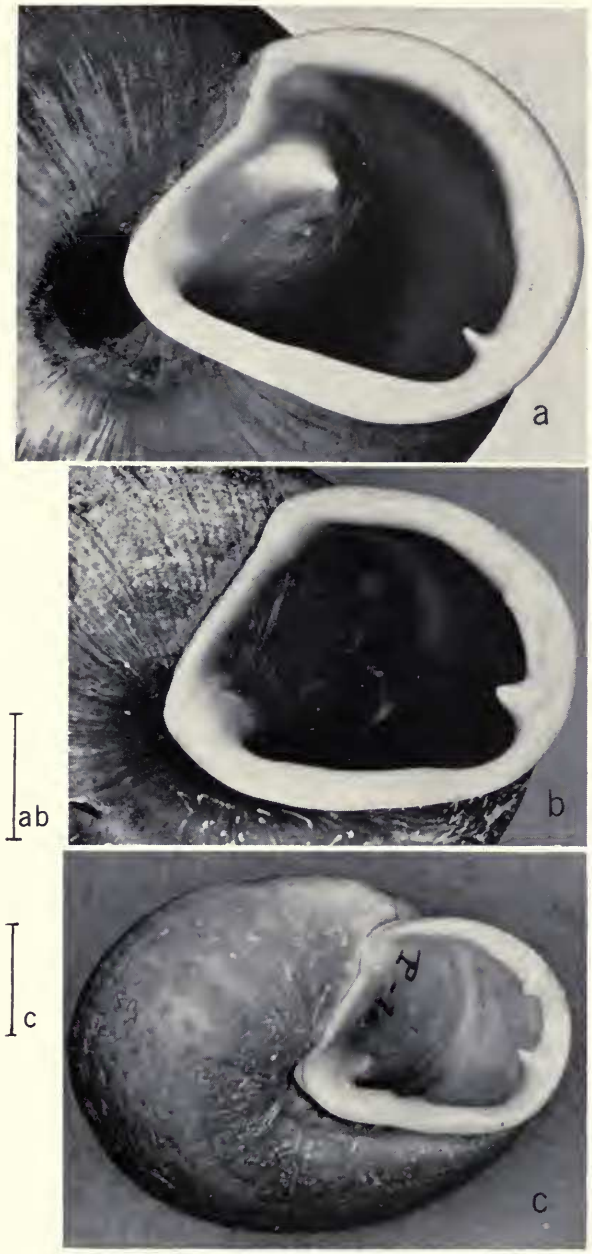


FIG. 49. Apertures of: *a*, *Isomeria oreas*, "Ecuador." Zurich, large; *b*, *Isomeria kolbergi*, Los Puentes, Ecuador, ANSP 61696. Holotype of *faunus ritchieana* Pilsbry, 1889; *c*, *Isomeria triodonta*, locality uncertain. Madrid. Scale lines equal 10 mm.

in that and two smaller sets is summarized in Table XIV. The distribution of diameter and H/D ratio is normal, but spread over a wide enough center in the case of the diameter to suspect that geographical, altitudinal or both types of variation will be found. Neither of the two specimens over 70 mm. in diameter had locality data.

	Diameter in mm.									
	44	47	50	53	56	59	62	65	68	71
No. of specimens	1	2	7	16	17	16	16	7	1	2

	H/D ratio				
	0.457	0.472	0.487	0.502	0.517
No. of specimens	2	0	5	11	20
	0.532	0.547	0.562	0.577	0.592
No. of specimens	19	15	6	4	3

The obtusely rounded periphery, wide umbilicus with its internal groove, conspicuous parietal lamellar tooth, single lower palatal tooth and presence of weak malleations at once separate this species. *I. fauna* differs in lacking the parietal tooth and in being acutely angulated; most of the other species have the umbilicus nearly closed and the teeth are quite different. While the Ecuadorean species are readily separable, it is easy to see how they could have been derived from *I. oreas* simply by making minor alterations in shell structure.

Isomeria kolbergi Miller, 1878. Figures 48c, 49b.

Isomeria kolbergi Miller, 1878, Malak. Blätt., **25**, pp. 167–168, pl. 8, fig. 2a, b —Valley of Pilatón, Ecuador (Boetzkes!); Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 257—Yungas, Ecuador (Cousin!).

Isomeria granulatissima Miller, 1878, Malak. Blätt., **25**, pp. 168–169, pl. 8, fig. 3—Nanegal, Ecuador (Wolf!); Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 255.

Helix (*Isomeria*) *faunus* var. *ritchieana* Pilsbry, 1889, Man. Conch. (2), **5**, p. 138, pl. 62, figs. 14–17—Pichincha, Northwest Ecuador.

Helix (*Isomeria*) *kolbergi* (Miller), Pilsbry, 1889, Man. Conch. (2), **5**, p. 148, pl. 43, figs. 46–47; Reibisch, 1896, Abhl. naturwiss. Gesell. Isis, Dresden, **7**, p. 56—Toachi Valley, Ecuador (Wolf!).

Helix (*Isomeria*) *granulatissima* (Miller), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 148–149, pl. 43, figs. 41–42; Reibisch, 1896, Abhl. naturwiss. Gesell. Isis, Dresden, **7**, p. 56—Cayandelet, Western Mts., Ecuador (Wolf!).

Pleurodonte (*Isomeria*) *kolbergi* Miller, Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Pleurodonte (*Isomeria*) *granulatissima* Miller, Pilsbry, 1894, *loc. cit.*

Pleurodonte (*Isomeria*) *faunus* var. *ritchieana* (Pilsbry), 1894, *loc. cit.*

Helix (*Isomeria*) *oreas* Germain, 1907 (not Koch, 1844), Bull. Mus. Nat. hist. nat., Paris, **13**, p. 53 (partly); Germain, 1910, Miss. Arc. de Méridien équatorial, **9** (3), pp. C12–C14 (partly).

Range.—Upper Río Esmereldas drainage; Central Ecuador from Ibarra to Cayandeled; Amazonian drainage from Río Quijos to upper Río Pastaza.

Material.—*Ecuador* (CNHM 40643): Val de Pilatón (CNHM 100094, ANSP 82701); Los Puentes, Val de Pilatón (CM 62.2587, ANSP 61696, type of *ritchieana*, ANSP 82700, CNHM 40634, CNHM 117850); Napo (CNHM 86683, CNHM 117848, CNHM 117849, Jackson 5297); Mera (CNHM 86695, Jackson 5517); "Alciagy" (CNHM 40635); Nanegal (USNM 307680, Paris—as *oreas*, ANSP); Topo (ANSP 186857, Jackson 7433); Puyo, 5,000–6,000 feet elevation (ANSP 170722, Jackson 6226); Gualea (MCZ 76516); Mt. Chimborazo (MCZ 87566); Cerro de Loma (Paris—as *oreas*); Milpe (Jackson 4817); Mindo (Jackson 4723); Santo Domingo de los Colorados (Jackson 9744); Ibarra (Jackson 9740); Nachiyacu between Baeza and Archidona (Jackson 4709); "Quito" (USNM 316048–316050, USNM 318223).

Diagnosis.—Umbilicus slightly to moderately open; basal lip with 0–2 low swellings or nodules; lower palatal lip with one conical, moderately prominent tooth situated on lip; upper palatal lip white, rarely with an indistinct swelling or small tooth; periphery acutely to obtusely carinated, usually acutely; surface with very fine radial sculpture, lightly to moderately malleated near the periphery; parietal callus with thick, raised edge; color liver brown to reddish brown, or with greenish-yellow mottlings; lip white. Diameter 41.5–63.3 mm. (mean 51.1 mm.), H/D ratio 0.445–0.572 (mean 0.499).

Remarks.—Pilsbry apparently had not seen any specimens of *kolbergi* when he described *ritchieana*, and would have been misled by Miller's description. *I. kolbergi* was described as having the last one-third whorl descending, gradually at first, then more rapidly. Only a very few specimens show this feature, most of them having a suddenly and sharply deflected aperture as is normal in *Isomeria*.

I. kolbergi is usually easily separated from *I. jacksoni* by its more widely open umbilicus and larger size. Form *granulatissima* differs only in having a distinct upper palatal tooth. Miller's cited differences of a "viel flachere Gestalt, das Fehlen der Rippen, der weitere Nabel" failing to hold when numerous specimens are examined. It is a rare mutant, being found in two of ten shells from Puyo, Ecuador (Jackson 6226) and one of three from Nachiyacu (Jackson 4709), but

did not occur in the large series of 37 specimens from Mera (Jackson 5517). Size variation is summarized in Table XIV.

The distribution is approximately the same as *I. cymatodes*, except for the fact that *kolbergi* extends further north and south than the recorded localities for *I. cymatodes*. Differences from *cymatodes* are fully covered in the discussion of the latter (p. 182).

Distribution of the diameters is normal, but there is a distinct bimodality in the obesity index.

	Diameter in mm.							
	43	46	49	52	55	58	61	64
No. of specimens	7	12	18	38	20	1	1	1

	H/D ratio				
	0.452	0.467	0.482	0.497	0.512
No. of specimens	7	17	17	16	11
	0.527	0.542	0.557	0.572	
No. of specimens	23	4	2	1	

The set from Puyo contains one of the high form and nine of the compressed variety; the large set from Mera (37 examples) has mostly the compressed variety. Since these two sets contained more than half of the available material, they easily could account for the bimodal distribution. Unfortunately, no other set contained more than three examples. Thus there is no data on the variation in material from other localities.

Possibly *I. fauna* (see p. 194) is a synonym. Until the Bogotá area can be revisited, however, it seems best tentatively to keep them distinct.

Isomeria triodonta (d'Orbigny, 1835). Figures 48d, 49c.

Helix triodonta d'Orbigny, 1835, Guerin's Mag. de Zool., **1835**, Class V, no. 61, p. 3—Guayaquil, Ecuador; d'Orbigny, 1837, Voy. Amer. Merid., Moll., pp. 234–235, pl. 24, figs. 1–3 (plate issued in 1836)—Puná, Guayaquil, Ecuador; Pfeiffer, 1848, Monog. helic. viv., **1**, p. 401; Reeve, 1854, Conch. Icon., *Helix*, pl. 208, fig. 1473; Pfeiffer, 1859, Monog. helic. viv., **4**, p. 309.

Helix atrata Reeve, 1852 (May), Conch. Icon., *Helix*, pl. 99, fig. 549—Puntophaya, Ecuador (Bourcier!).

Isomeria triodonta (d'Orbigny), Miller, 1878, Malak. Blätt., **25**, p. 170; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 258.

Isomeria mauritii (sic) Jousseaume, 1887, Bull. Soc. Zool. France, **12**, pp. 180–181—New name for *Helix atrata* Reeve, 1852, not *Helix atrata* Pfeiffer, 1854.

Isomeria mauricei Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 256—Emendation of *mauritii* Jousseaume, 1887.

Helix (*Isomeria*) *mauritii* (Jousseaume), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 145–146, pl. 44, fig. 7.

Helix (*Isomeria*) *triodonta* d'Orbigny, Pilsbry 1889, *loc. cit.* (2), **5**. p. 152, pl. 47, figs. 33–35.

Helix (*Isomeria*) *atrata* var. Kobelt, 1893, Syst. Conch. Cab., I (12), **4**, p. 631, pl. 181, figs. 3–6 (plate issued in 1886).

Pleurodonte (*Isomeria*) *mauritii* (Jousseaume), Pilsbry, 1894, Man. Conch. (2) **9**, p. 94.

Pleurodonte (*Isomeria*) *triodonta* (d'Orbigny), Pilsbry, 1894, *loc. cit.* (2), **9**, p. 94.

Range.—Unknown, since the only reported locality, Puná Island near Guayaquil, is merely the place where the type was purchased.

Material.—*Ecuador* (CNHM 40641, CNHM 40650, CNHM 100093, CNHM 132556, ANSP 64441, ANSP 78357, USNM 57282, USNM 307656, USNM 316052, Edinburgh, Zurich): Guayaquil (USNM 307492 ex Deyrolle).

Diagnosis.—Basal lip with two close-set teeth near umbilicus, occasionally fused; lower palatal lip with prominent, white-tipped conical tooth; upper palatal lip with weak to usually prominent white-tipped tooth placed on or just above periphery; umbilicus usually with a slight lateral crack, occasionally imperforate; surface finely rib-striated, often heavily malleated on later whorls; parietal callus very thin, rarely with a raised white lip edge; periphery right to obtusely angled, occasionally protruding; color liver-brown, lip mainly brown, often with basal and part of upper palatal portions white. Diameter 39.2–51.8 mm. (mean 44.9 mm.), H/D ratio 0.481–0.667 (mean 0.547).

Remarks.—Most collections have two forms separated, the smaller one called *triodonta* and the larger *atrata*. Available material does show a bimodal distribution of the diameter, but the importance of the difference cannot be assessed in the absence of localized collections. The total range is no larger than that found in other species of *Labyrinthus* and *Isomeria* and easily could reflect populations from

	Diameter in mm.						
	40	42	44	46	48	50	52
No. of specimens	8	8	9	4	5	8	2

	H/D ratio				
	0.490	0.510	0.530	0.550	0.570
No. of specimens	2	8	9	9	11
	0.590	0.610	0.630	0.650	0.670
No. of specimens	2	2	0	0	1

dry and wet areas. There is no similar, bimodal distribution of the obesity index. In large and small sized populations of such species as *Labyrinthus otis orthorhinus*, there is no significant variation in H/D ratio.

Neither of the two recorded localities can be considered reliable. Reeve's citation (*loc. cit.*) of "Puntophaya" is the type locality of *Helix atrata* Pfeiffer, 1854 (= *Isomeria jacksoni* Solem, 1966, see p. 178), not Reeve, 1852 and probably has no reference to the mislabeled *I. triodonta* figured by Reeve. The type of *triodonta* was purchased by a ship's surgeon at Puná, Ecuador from a native who was wearing it as a single ornament suspended on a thong around his neck. The fact that it was worn as a single ornament suggests that it was a valued item obtained in trade rather than an object easily picked up locally. Similarly, the single specimen from "Guayaquil" (USNM 307492 ex Deyrolle) probably had the locality added by Deyrolle on the basis of the type locality.

There is some variation in the degree of carination and the extent to which malleations appear on the whorls. It seems obvious that the museum specimens have come from several populations. Sometimes *I. triodonta* and *I. aequatoria* are confused. The latter has a smoothly closed umbilicus, no malleations, is smaller, and the upper palatal tooth is only a slight triangular projection; *I. triodonta* has the umbilicus slightly open or sealed by a secondary callus, is malleated on the later whorls, is larger, and has a lamellar upper palatal tooth.

Isomeria stoltzmanni (Lubomirski, 1879). Figure 50a–e.

Helix (*Isomeria*) *stoltzmanni* Lubomirski, 1879, Proc. Zool. Soc. London, **1879**, p. 720, pl. 55, figs. 4–6—Montana de Palto, near Tambillo, District of Chota, Peru (Stoltzmann!).

Helix (*Isomeria*) *stoltzmanni* Lubomirski, Pilsbry, 1889, Man. Conch. (2), **5**, p. 150, pl. 57, figs. 28–30.

Pleurodonte (*Isomeria*) *stoltzmanni* (Lubomirski), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Known only from the type locality.

Material.—Peru: CAJAMARCA—Montaña de Palto, near Tambillo, District Chota, Peru (Warsaw, holotype and paratype).

Diagnosis.—The basal lip with 0–2 slight swellings near umbilicus; lower palatal lip with a very small conical tooth; upper palatal lip sinuated and somewhat thickened; umbilicus only slightly covered by basal and parietal lips; periphery nearly right angled; parietal

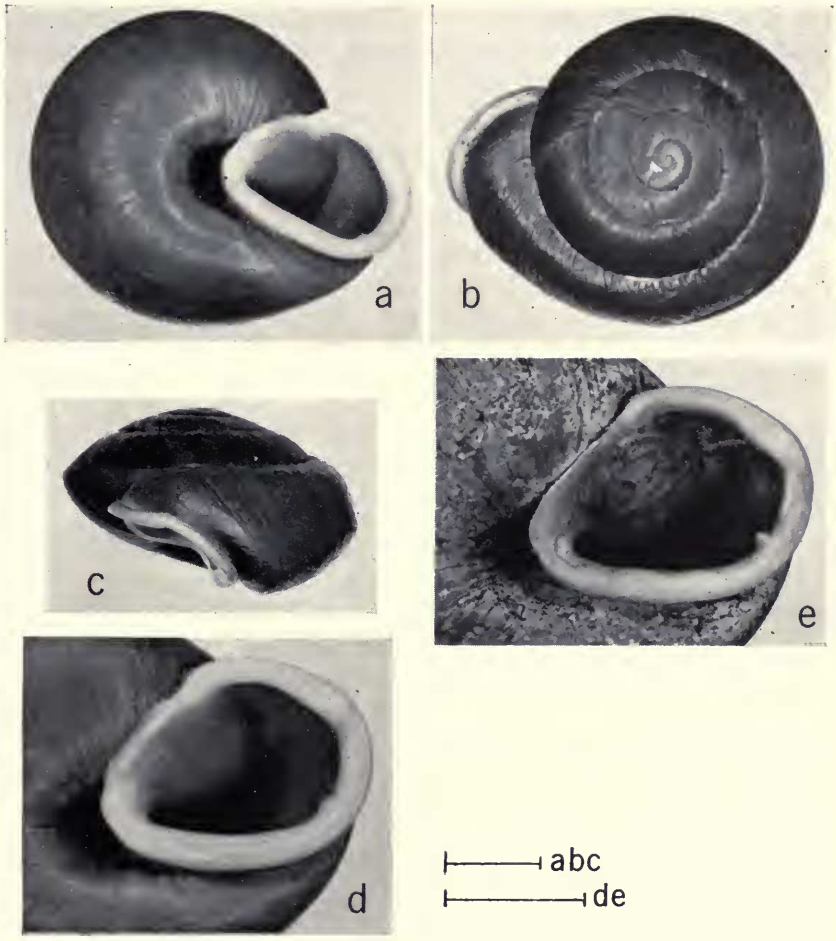


FIG. 50. *Isomeria stoltzmanni*, Montana de Palto, near Tambillo, District Chota, Peru. Polska Akademia Nauk. Holotype. *a*, base; *b*, top; *c*, side; *d*, aperture of holotype; *e*, aperture of paratype. Scale lines equal 10 mm.

callus with very heavy raised edge; surface with strong radial growth striae and grooves, but no trace of malleations; lip white on inner margins, slightly brown tinted on outer. Diameter 39–40 mm., H/D ratio 0.487–0.495, umbilical opening contained 12–14 times in the diameter.

Remarks.—Apparently the nearest relative is *I. kolbergi* from Ecuador. *I. stoltzmanni* is a smaller, heavier shell, completely lacks malleations on the body whorl, has the palatal tooth much smaller

and part of the lip is tinted brown. *I. kolbergi* may be only subspecifically separable, but in the absence of material from intermediate areas, no judgment can be made.

The exact location of the type locality is uncertain. The Cerro de Palto is not in Chota District and is quite far from the two towns of Tambillo in Cajamarca, both of which are near Chota District but not within the present boundaries.

Through the kind cooperation of Dr. A. Riedel of the Polska Akademia Nauk it was possible to examine the type and one paratype. The original figures were rather distorted and the type is refigured and redescribed. A new description of the type follows:

Shell of average size, carinated, with slightly more than 4¾ whorls. Coiling of early whorls normal, last half of body whorl compressed laterally with reduced carination. Spire rather strongly elevated, slightly rounded above, H/D ratio 0.487. Apex with widely spaced radial growth lines, becoming finer and very crowded on spire. Surface of lower spire and body whorl with prominent granulations that are arranged in linear series on constricted portion of body whorl and are greatly reduced in size on base of shell. Periphery acutely angulated, nearly right angled, slightly protruded. Color greenish-yellow brown, lighter behind lip. Upper palatal lip and parietal callus white, lower palatal and basal lips with brownish tints on outer edge. Umbilicus narrowly open, contained 14 times in the diameter, with columellar groove clearly visible. Aperture ovate, very strongly deflected, inclined about 75° from the shell axis, descending abruptly with deep, narrow posterior indention. Parietal wall without dentition, but with a rather broad, raised callus, narrower in center, edges wider and elevated at upper corner. Basal lip strongly reflected, thickened and elevated internally; lower palatal lip thickened and reflected with low conical knob surmounting lip and trace of peripheral groove at upper margin; upper palatal lip somewhat sinuated, thickened, but less broadly reflected. Height of holotype 19.0 mm., diameter 39.0 mm.

The paratype differs in having a straight raised edge to the parietal callus, a much more fully developed lower palatal tooth and two faint rounded bumps on the basal lip near the umbilicus (fig. 50e).

Isomeria jacksoni new name. Figures 51a, 52a.

Helix atrata Pfeiffer, 1854 (not Reeve, May 1852), Proc. Zool. Soc. London, **1852**, p. 153—Puntophaya, Ecuador (Bourcier!); Pfeiffer, 1853, Monog. helic. viv., **3**, p. 258; Pfeiffer, 1854, Syst. Conch. Cab., I (12), **3**, p. 366,

pl. 139, figs. 1–2 (plate issued in 1852); Hidalgo, 1870, Jour. de Conch., **18**, p. 31—Macas and Napo, Ecuador; Hidalgo, 1870, Moluscos del Viaje al Pacifico, pp. 12–13; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 464; von Martens, 1885, Conch. Mitteil., **2** (5–6), p. 156—Rio del Ciuto at Pichincha, Ecuador at 1,300–1,400 meters elevation (Stübel!).

Isomeria atrata (Pfeiffer, not Reeve, 1852), Miller, 1878, Malak. Blätt., **25**, p. 167; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 254—San Domingo, trail from Aloag to Chones, Ecuador (Cousin!).

Helix (Isomeria) atrata Pfeiffer (not Reeve, 1852), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 144–145, pl. 44, figs. 3–4.

Pleurodonte (Isomeria) atrata (Pfeiffer) (not Reeve, 1852), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Upper Esmereldas and Amazonian drainages in Central Ecuador.

Material.—Ecuador: "Andes of Ecuador" (USNM 516773); near Nanegal (ANSP); Mera (CNHM 85385, Jackson 9364); Topo (Jackson 10915); Puyo (Jackson 6820); Sigchos (Jackson 9728); Ibarra (Jackson 9678).

Diagnosis.—Basal lip with single low swelling; lower palatal lip with small conical tooth; umbilicus slightly open; periphery obtusely carinated; surface with very fine growth striae and granulations but no malleations; parietal callus with thick raised edge; color dark reddish-brown or with many scattered, irregular greenish-yellow maculations. Diameter 32.2–45.4 mm. (mean 40.0 mm.), H/D ratio 0.468–0.553 (mean 0.517).

Remarks.—Most authors have realized that the *Helix atrata* of Reeve and Pfeiffer were distinct species, but no substitute has been proposed for Pfeiffer's homonym. Great pleasure is taken in dedicating this species to Ralph Jackson of Cambridge, Maryland, whose unrivaled collection of South American non-marine mollusks has made much of this study possible and in token recognition of his great help to many malacologists.

The possibility exists that this is a dwarf race of *I. kolbergi*, perhaps equivalent to the dwarf form of *L. raimondii*. The few known specimens, however, are easily separable from specimens of *I. kolbergi* taken at the same locality by the more covered umbilicus, thicker, more solid shell, much smaller size and slightly fewer whorls. Until the ecology of the two is studied, I'd prefer to keep them as distinct species. The extent of the size difference can be appreciated by noting the comparison in Table XIV, between sets of *kolbergi* and *jacksoni* from the same locality.

The few specimens from scattered localities are almost all in the collection of Ralph Jackson. Variation is summarized in Table XIV. No data on elevations is available.

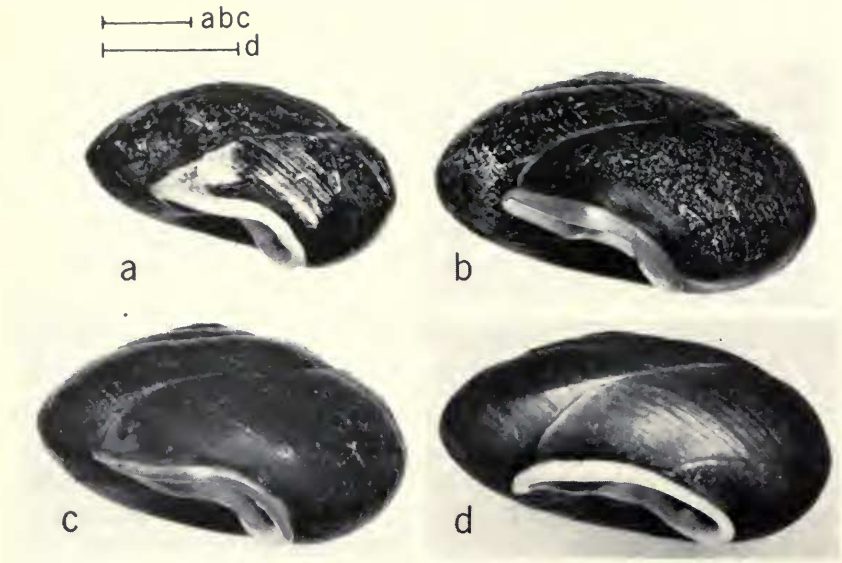


FIG. 51. Shells of: *a*, *Isomeria jacksoni*, Mera, Ecuador, CNHM 85385; *b*, *Isomeria cymatodes*, Puyo, Ecuador, CNHM 86692; *c*, *Isomeria cymatodes* form *parietidentata*, Val de Pilatón, Ecuador, CNHM 60801; *d*, *Isomeria fordiana*, Marmato, Colombia, ANSP 33133. Holotype. Scale lines equal 10 mm.

Isomeria cymatodes (Pfeiffer, 1852). Figures 51b–c, 52b.

Helix cymatodes Pfeiffer, 1852, Zeitschr. f. Malak., **9** (5), p. 92—locality unknown; Pfeiffer, 1853, Monog. helic. viv., **3**, p. 208—Ecuador; Hidalgo, 1870, Moluscos del Viaje al Pacifico, p. 11, pl. 2, figs. 1, 3—Napo, Ecuador (Martinez!).

Isomeria cymatodes (Pfeiffer), Miller, 1878, Malak. Blätt., **25**, p. 169—Nanegal (Wolf!), Val de Pilatón (Boetzkes!), Ecuador; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 255—Los Puentes, Canton de Quito, Ecuador (Cousin!).

Helix (*Isomeria*) *cymatodes* Pfeiffer, von Martens, 1885, Conch. Mitteil., **2** (5–6), p. 156—Nanegal, Ecuador at 1,000–2,000 meters elevation (Stubel!); Pilsbry, 1889, Man. Conch. (2), **5**, pp. 146–147, pl. 46, figs. 24–26.

Isomeria parietidentata Miller, 1878, Malak. Blätt., **25**, pp. 169–170—Val de Pilatón, Ecuador (Boetzkes!); Miller, 1879, *op. cit.*, n. f., **1**, pl. 5, figs. 3a–c; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 258—trail from Aloag to Chones, Megia, Ecuador (Cousin!).

Helix (*Isomeria*) *parietidentata* (Miller), Pilsbry, 1889, Man. Conch. (2), **5**, pp. 147–148, pl. 61, figs. 11–13.

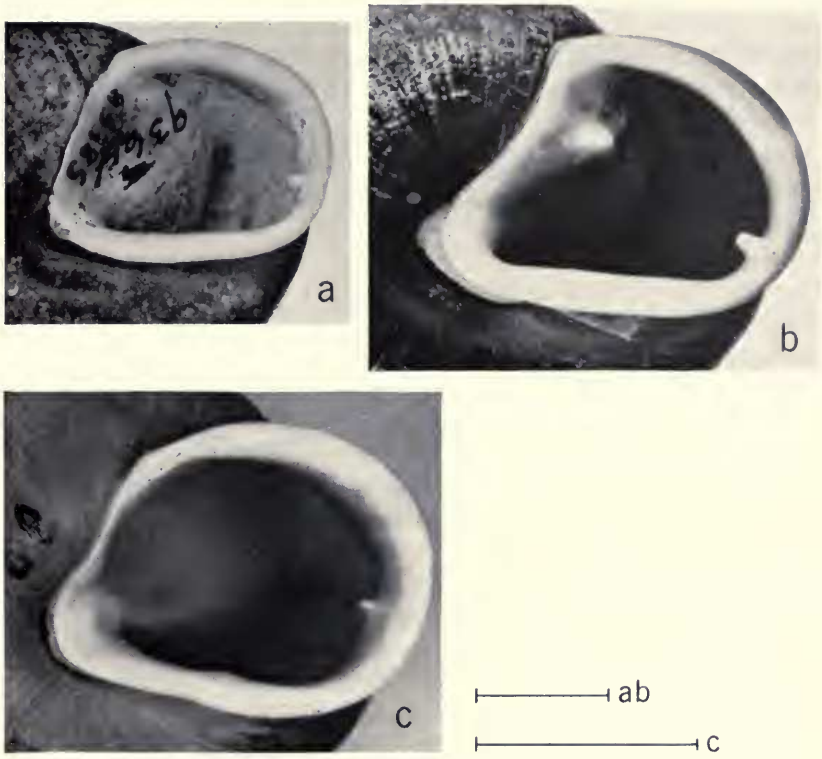


FIG. 52. Apertures of: *a*, *Isomeria jacksoni*, Mera, Ecuador, CNHM 85385; *b*, *Isomeria cymatodes*, Puyo, Ecuador, CNHM 86692; *c*, *Isomeria fordiana*, Marmato, Colombia, ANSP 33133. Holotype. Scale lines equal 10 mm.

Pleurodonte (*Isomeria*) *cymatodes* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Pleurodonte (*Isomeria*) *parietidentata* (Miller), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Helix (*Isomeria*) *oreas* Germain, 1907 (not Koch, 1844), Bull. Mus. Nat. hist. nat., Paris, **13**, p. 53—Nanegal, Horongo, Ecuador (partly); Germain, 1910, Miss. Arc de Méridien équatorial, **9** (3), pp. C12–C14—partly.

Range.—Upper Napo and Pastaza Rivers on the Amazonian slopes and the upper Rio Esmereldas basin on the Pacific slopes at 3,900–7,800 feet elevation.

Material.—Ecuador (Zurich, Edinburgh, ANSP 33136): "Quito" (Zurich, USNM 316051, USNM 317440, ANSP 30643); Nanegal (CNHM 102414, USNM 307443, ANSP); Mera (CNHM 86693, Jackson 10893, Jackson 5521); Napo (CNHM 86694, CNHM 117856,

Jackson 5299); Puyo (CNHM 86692, ANSP 170729, Jackson 9337); San Nicholas (CNHM 40639, ANSP 60197); Val de Pilatón (CM 62.2585, CNHM 60801); Topo (Jackson 8821); Sigchos, west of Latacunga (Jackson 9730).

Diagnosis.—Basal lip with 0–2 inconspicuous bumps; parietal wall with small lamellar to conical denticle; lower palatal lip with high conical tooth situated on lip; umbilicus nearly closed by extension of basal and parietal lips, closed rest of way by an accessory plate that is occasionally broken or missing; periphery obtusely angulated; surface with fine radial striae, very heavily malleated on lower whorls near periphery; color dark reddish-brown to light reddish-brown, occasionally speckled with greenish-yellow; lip white on basal margin, brownish tinted on part of upper palatal lip; parietal callus very thin with high, raised edge. Diameter 39.9–56.2 mm. (mean 50.0 mm.), H/D ratio 0.464–0.581 (mean 0.502).

Remarks.—Occasionally specimens with a very small parietal tooth can be confused with *I. kolbergi.* The latter lacks a parietal tooth, has a pure white lip, generally a moderately open umbilicus, more sharply carinated periphery, weaker malleations and 5⅛ to 5¾ whorls (rarely 5). In contrast, *I. cymatodes* has a small to large parietal tooth, brown markings on the outer part of the upper palatal lip, generally a completely closed umbilicus, obtusely angulated periphery, heavy malleations and only 4¼ to 4¾ whorls (rarely 5). The secondary closure of the umbilicus by formation of an accessory plate is unique and easily separates *I. cymatodes* from *I. oreas.*

In the shell collection at the Muséum National d'Histoire Naturelle, Paris, *cymatodes* and *kolbergi* are completely confused and mingled, with the Ecuador material reported by Germain as *oreas* being a mixture of the former two species.

If only a few specimens are available for study, a division into *cymatodes* and *parietidentata* becomes feasible. As soon as series of specimens are examined, the separation becomes untenable. The differentiating characters of *parietidentata* are a more broadly expanded lip, shallower posterior gutter behind the lip, more sharply deflected aperture (see fig. 51c). The longer sets from Mera and Puyo contain intergrades and indicate that *parietidentata* is an individual variation.

All reported localities are from the Upper Río Esmereldas drainage on the Pacific slopes or the Río Napo and Río Pastaza drainages on the Amazonian side. The only cited elevation record is 3,900–7,800 feet elevation near Nanegal.

Size and shape variation is not very large. The distribution of the diameter suggests that dwarfed populations exist, since the curve is obviously skewed. The distribution of the obesity suggests that an occasional individual is exceptionally elevated. The four smallest shells are a pair from Mera (Jackson 10893) and Sigchos (Jackson 9730) from opposite sides of the Andes. One of the Sigchos examples is also the most elevated specimen, but the other small shells are normally elevated.

Diameter in mm.	40	42	44	46	48	50	52	54	56
No. of specimens	2	2	5	8	14	18	30	13	3

H/D ratio	0.467	0.482	0.497	0.512	0.527
No. of specimens	9	19	26	24	12
H/D ratio	0.542	0.557	0.572	0.587	
No. of specimens	1	3	0	1	

Variation in several sets is summarized in Table XV.

Isomeria fordiana (Pilsbry, 1889). Figures 51d, 52c.

Helix (*Isomeria*) *fordiana* Pilsbry, 1889, Man. Conch. (2), **5**, pp. 141–142, pl. 62, figs. 18–21—Marmato, Colombia.

Pleurodonte (*Isomeria*) *fordiana* (Pilsbry), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—One locality each in the Cauca and Magdalena drainages.

Material.—Colombia: CALDAS—Marmato (ANSP 33133, types); NORTE DE SANTANDER—?Ocaña (Zurich ex Wallis 1875).

Diagnosis.—Basal lip with broad, low knob; lower palatal lip with small conical white-tipped tooth; umbilicus with barely open crack; periphery nearly right angled; parietal callus thin with raised edge; lip broad, brown inside, white on edge, strongly indented behind; surface with faint granulations and radial growth lines, but no malleations. Diameter 39.5–42.4 mm., H/D ratio 0.488–0.492.

Remarks.—The umbilical closing is as in *I. cymatodes,* but the lack of a parietal tooth and absence of malleations on the body whorl at once separate the two species. *I. fauna* differs in having malleations, a distinctly open umbilicus, right-angled periphery and in being larger.

Isomeria scalena (Martens, 1881). Figures 53c–e, 54c.

Helix (*Isomeria*) *scalena* Martens, 1881, Conch. Mitteil., **2** (5–6), pp. 156, 170–172, pl. 31, figs. 1–3—Cerro Pelado, La Plata, Colombia at 2,300 meters elevation (Stübel!).

Helix (Isomeria) scalena Martens, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 143–144, pl. 61, figs. 1–3.

Pleurodonte (Isomeria) scalena (Martens), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—La Plata drainage of Huila, Colombia at 7,550–7,875 feet elevation.

Material.—Colombia: HUILA—Río Páez Valley, 2,400 meters elevation (USNM 251175); Hacienda Medersenberg, La Plata (SMF 172173, CNHM 133152 E. Kohldorfs!).

Diagnosis.—Aperture without teeth although basal lip greatly thickened; umbilicus nearly covered by lip extensions, almost completely closed by a secondary callus; periphery acutely angulated or right angled; surface with prominent rib-striae, weakly malleated near periphery; parietal callus with elevated edge. Diameter 43–55 mm.

Remarks.—The larger size, nearly closed umbilicus and total absence of dentition separate *scalena* from the other known species of *Isomeria*. Of the toothless species, *basidens* and *neogranadensis* are much smaller and have a very obtusely angulated periphery; *meyeri* is much smaller, has the umbilicus closed by the expansion of the basal and parietal lips, and the lip is yellowish; while *anodonta* has the umbilicus widely open, the surface smooth without trace of angulation and is dull brown.

The five specimens (diameter 43–50.7 mm., mean 47.2 mm., H/D ratio 0.492–0.563, mean 0.518) from La Plata and the Rio Páez, a tributary of the Río La Plata that drains the slopes of Cerro Pelado and forms the headwaters of the Río Magdalena, are much smaller than the type (diameter 55 mm., H/D ratio 0.528). The umbilical callus of *I. scalena* is the same as in *I. fordiana* and *I. cymatodes*, but the former differs in having a lower palatal tooth, a basal knob, and the aperture much more sharply deflected. The latter is much more heavily malleated and with several denticles.

All localities are part of the same drainage system and are only a few miles apart. The three shells from Hacienda Medersenberg are larger (diameter 48–50.7 mm.) than those from the Río Páez (diameter 43–44.1 mm.).

Isomeria aequatoriana (Hidalgo, 1867). Figures 53a, 54a–b, 55a–c.

Helix aequatoriana Hidalgo, 1867, Jour. de Conchy., **15**, pp. 307–308, pl. 8, fig. 2—Ecuador; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 500; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 361.

TABLE XV.—Size and shape variation in *Isomeria cymatodes*, *I. aequatoriana* and *I. globosa*

Species and set	No. of specimens	Height			Diameter			H/D ratio			D/U ratio		
		Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.	Mean	Range	S.E.M.
I. cymatodes													
Jackson 5521; Mera, Ecuador	40	25.4	21.5–29.2	0.25	50.4	44.6–55.1	0.41	0.504	0.469–0.564	0.003			
Jackson 8821; Topo, Ecuador	5	25.6	24.9–27.0	0.42	51.5	50.3–53.5	0.58	0.496	0.482–0.517	0.007			
Jackson 9337; Puyo, Ecuador	11	26.1	25.0–27.9	0.24	52.3	51.2–54.7	0.32	0.498	0.468–0.515	0.004			
I. aequatoriana													
USNM 426539; Méndez, Ecuador	12	24.8	22.3–27.5	0.41	47.2	43.6–51.5	0.60	0.525	0.489–0.569	0.007			
Jackson 6227 and MCZ 195875; Puyo, Ecuador	7	27.8	25.9–29.3	0.47	55.2	51.3–58.0	0.94	0.504	0.482–0.523	0.006			
Jackson 6994, MCZ; Mera, Ecuador	17	27.9	25.9–33.8	0.49	55.2	50.2–68.2	1.25	0.506	0.440–0.545	0.007			
Jackson, 7435, MCZ; Topo, Ecuador	7	28.1	25.6–30.2	0.57	55.9	53.7–58.4	0.59	0.503	0.472–0.517	0.006			
I. globosa													
Jackson 7853; Mera, Ecuador	18	22.0	20.3–23.7	0.20	42.7	39.5–44.4	0.30	0.515	0.482–0.558	0.004	25.8	17.5–36.6	1.33

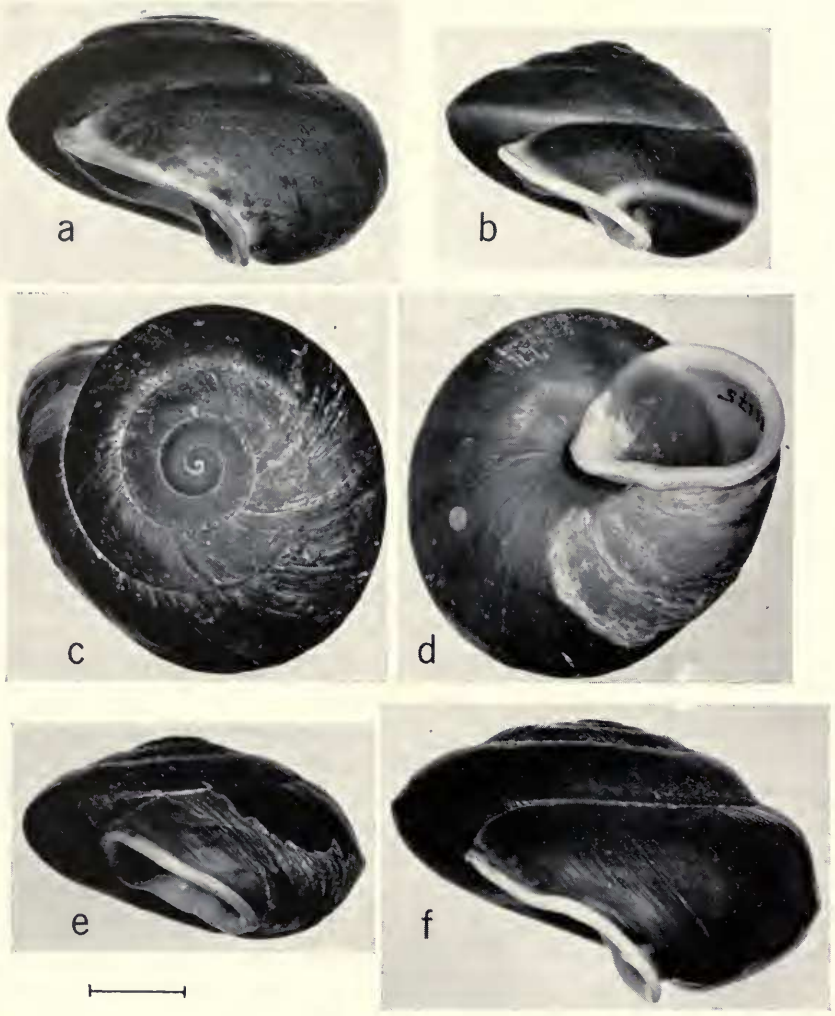


FIG. 53. Shells of: *a*, *Isomeria aequatoriana*, Topo, Ecuador, CNHM 86677; *b*, *Isomeria globosa*, Mera, Ecuador, CNHM 86700; *c–e*, *Isomeria scalena*, Rio Paez Valley, 2,400 meters elevation, Colombia, USNM 251175 (*c*, top; *d*, base; *e*, side); *f*, *Isomeria fauna*(?), Santa Fe de Bogotá, Colombia. Zurich. Scale line equals 10 mm.

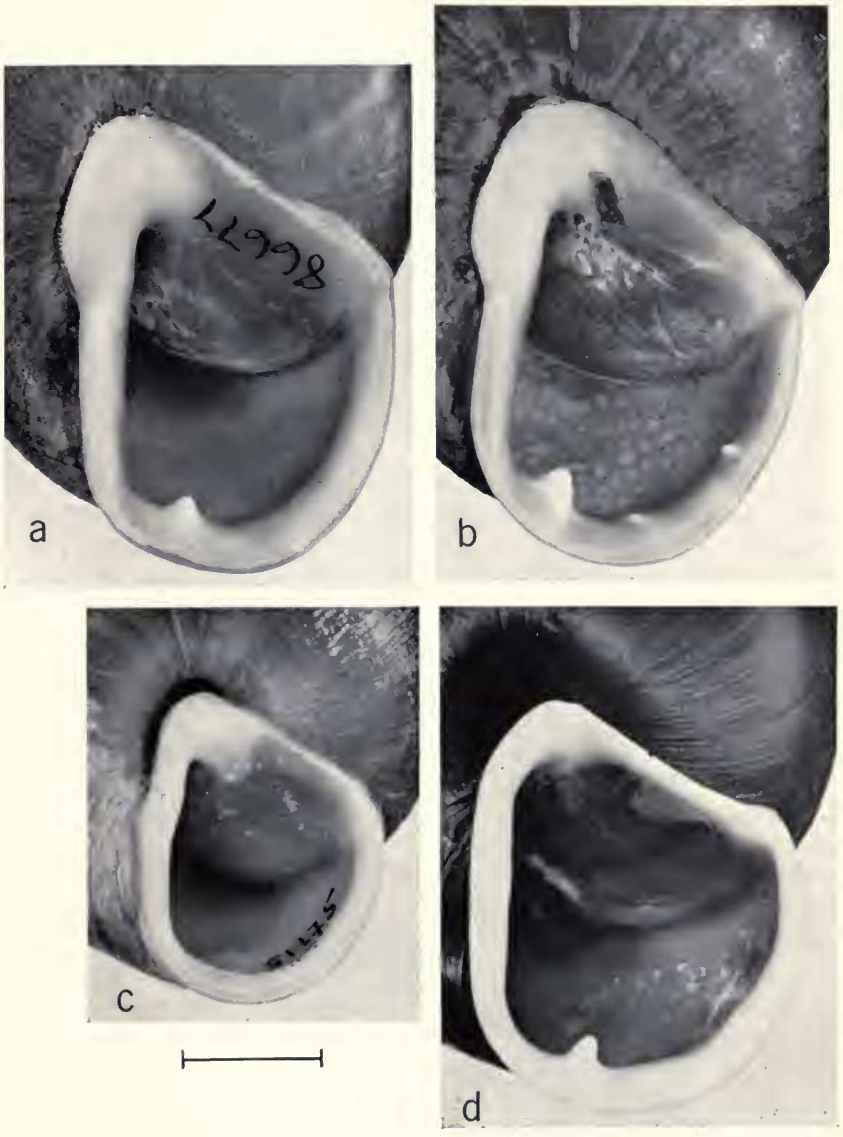


FIG. 54. Apertures of: *a–b*, *Isomeria aequatoriana*, Topo, Ecuador, CNHM 86677 (*a*, normal form; *b*, with extra palatal teeth); *c*, *Isomeria scalena*, Rio Paez Valley, 2,400 meters elevation, Colombia, USNM 251175; *d*, *Isomeria fauna*(?), Santa Fe de Bogotá, Colombia. Zurich. Scale line equals 10 mm.

Isomeria aequatoriana (Hildalgo), Miller, 1878, Malak. Blätt., **25**, p. 167; Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 254.

Helix (*Isomeria*) *aequatoriana* Hidalgo, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 142–143, pl. 47, fig. 39.

Pleurodonte (*Isomeria*) *aequatoriana* (Hidalgo), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Helix (*Isomeria*) *wolfi* Reibisch, 1896, Abhl. naturwiss. Gesell. Isis., Dresden, **7**, pp. 56–57—Machai (=Macas), Valley of the Rio Pastaza, Ecuador at 4,900 feet elevation (Wolf!).

Range.—Amazonian slopes of Ecuador from Rio Napo south to upper Paute River. Reported from 3,900–4,900 feet elevation.

Material.—Ecuador (USNM 316053, ANSP 45556, ANSP 63586, CNHM 40637, CNHM 102430): Rio Pastaza at 1,000 meters elevation (CNHM 117852, CNHM 117853, CNHM 117855); Napo (CNHM 86682, Jackson 5448, CNHM 117851); Mera (CNHM 86697, ANSP 175412, MCZ 195872, Jackson 6994); Topo (CNHM 86677, Jackson 7435, CNHM 117854, MCZ 193302, MCZ 193310); Méndez, Upper Paute Valley (USNM 426539, CNHM 71046); Chiquaza (ANSP); Oriente Prov. (USNM 628793); Abitagua, Pastaza Valley (Jackson 5718); 30 miles east of Baños (MCZ 96928); Loreto at 550 meters (SMF 156312); Puyo (Jackson 6227, MCZ 195875); Nachiyacu (MCZ 139960).

Diagnosis.—Lower palatal lip with conical white tooth; upper palatal lip rarely with one or two small denticles or swellings; umbilicus usually completely closed by extension of lips, but occasionally with a moderate to wide lateral crack; periphery usually obtusely angulated; surface with very fine radial striae and granulations, but no malleations; lip brown tinted; parietal callus thin; lip broadly and slightly elevated; color light liver-brown, usually with numerous fine yellowish flecks. Diameter 43.6–71 mm. (mean 54.1 mm.), H/D ratio 0.441–0.569 (mean 0.509).

Remarks.—The usually closed umbilicus, lack of any malleations or a parietal tooth, presence of only a lower palatal tooth (occasionally one or two accessory palatal denticles) and brown lip easily identify this species. No authentic material of the unfigured *wolfi* (diameter 52–57 mm.) was examined, but material from the Rio Pastaza was unquestionably *aequatoriana* and no hesitation is felt in synonymizing the two. The original description of *wolfi* is translated below for convenient reference:

> Shell almost lenticular, thick, obtusely keeled, with covered umbilicus. Whorls convex, five in number. Sutures fairly shallow near apex, becoming progressively deeper toward aperture so that whorls become more convex. Last

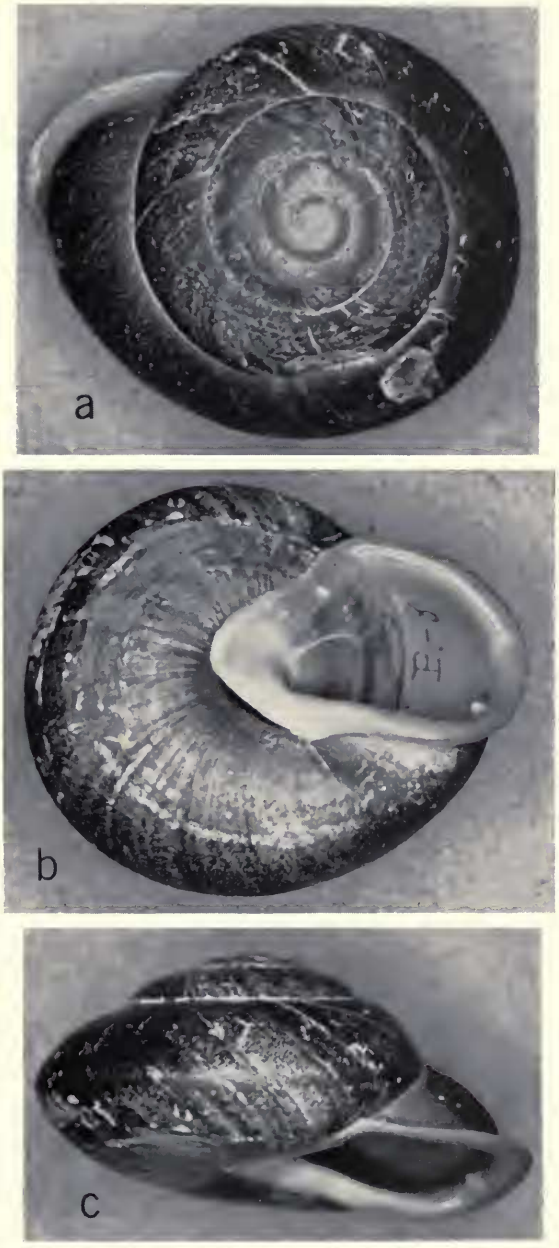


FIG. 55. Type specimen of *Isomeria aequatoriana*. *a* top; *b*, base; *c*, side. Ecuador. Madrid. Holotype.

whorl deflected for about 5 mm. suddenly before aperture. Umbilical callus area impressed, convexity of whorls gradually increasing from upper edge of aperture to base. Upper surface finely grooved. Both surfaces with fine granulations and wrinkles, which appear white from erosion. Aperture very oblique, proportion of breadth to length about 2:3. Lip slightly reflected above, more laterally and strongly basally, completely covering umbilicus. Upper and outer lip edges evenly curved, but sinuated basally. Medial portion bent a little upward, rest almost straight. Inner edge of palatal lip with white-tipped conical tooth. Some specimens with one or two small teeth placed above this tooth. Lip yellow brown, lighter near umbilical callus, which is almost white. Shell brown in fresh specimens, liver colored in dead examples. Parietal wall with thin, shining callus joining ends of the lips. Measurements—diameter 52–57 mm., height 21–23 mm.

This is an excellent description of *aequatoriana*.

The recorded localities are all from the Upper Amazonian basin from the Río Napo south to the upper Paute River. It is not known how far into the lowlands it extends, the recorded elevations being 1,800–4,900 feet.

Size variation is rather extensive, the distribution of the diameter being strongly affected by the set from Méndez (USNM 426539, CNHM 71046) which contained 11 of the 14 specimens with a diameter of less than 49.5 mm. Other sets from Mera and Puyo averaged much larger (see Table XV), although no material reached the size of the type specimen (71 mm.). Variation in the H/D ratio, as usual, was much less striking.

Diameter in mm.	45	48	51	54	57	60	63	66	69
No. of specimens	6	8	11	20	18	6	0	3	1
H/D ratio	0.447		0.462		0.477		0.492	0.507	
No. of specimens	2		2		7		11	17	
H/D ratio	0.522		0.537		0.552		0.567		
No. of specimens	22		8		2		1		

During a study trip to Madrid, sponsored by the National Science Foundation and Field Museum of Natural History, the probable type of *Helix aequatoriana* was located and photographed (fig. 55).

It is quite possible that the unrecognizable *I. calomorpha* (Jonas, 1839) is *I. aequatoriana*. The size of the former (diameter 62 mm.) and its general appearance are rather similar, but it seems best to consider *calomorpha* a *nomen dubium* (see p. 139).

Isomeria globosa (Broderip, 1832). Figure 56a–b.

Carocolla globosa Broderip, 1832, Proc. Zool. Soc. London, **1832**, p. 30—woods on Tumaco Id., West Colombia.

Helix subcastanea Pfeiffer, 1842, Symbolae hist. heliceorum, **2**, p. 103—New name for *Carocolla globosa* Broderip, 1832, not *Helix globosa* Sowerby, 1818, an unnecessary proposal; Pfeiffer, 1848, Monog. helic. viv., **1**, p. 401; Reeve, 1852, Conch. Icon., *Helix*, pl. 99, fig. 543.

Isomeria subcastanea (Pfeiffer), Miller, 1878, Malak. Blätt., **25**, pp. 170–171—Val de Pilatón, Pisagua, Milagro, Ecuador at 500–1,500 meters elevation (Boetzkes!); Miller, 1879, *op. cit.*, n.f., **1**, pp. 117–118—forests of Rio Esmereldas, Prov. Esmereldas, Ecuador at 0–300 feet elevation (Wolf!); Cousin, 1887, Bull. Soc. Zool. France, **12**, p. 258—trail from Aloag to Chones, Canton Megia, Ecuador (Cousin!); Gude, 1900, Jour. of Malac. **7** (6), pp. 144–146, figs. 3–4—Paramba, Ecuador at 3,500 feet elevation (Rosenberg!).

Helix (*Isomeria*) *subcastanea* Pfeiffer, Pilsbry, 1889, Man. Conch. (2), **5**, p. 157, pl. 44, figs. 8–10; Kobelt, 1894, Syst. Conch. Cab., I (12), **4**, pp. 630–631, pl. 181, figs. 1–2; Reibisch, 1896, Abhl. naturwiss. Gesell. Isis., Dresden, **7**, p. 56—Bulubulu Mt. and Manabi, Ecuador (Wolf!).

Pleurodonte (*Labyrinthus*) *subcastanea* (Pfeiffer), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Isomeria subcastanea var. *kobeltiana* Gude, 1900, Jour. of Malac., **7** (6), pp. 144–146, figs. 1–2—Ecuador.

Helix (*Isomeria*) *equestrata* Germain, 1907 (not Moricand, 1858), Bull. Mus. national hist. nat., Paris, **13**, p. 53—Albañín, Río Jubones Valley and Cerro de Castello, Mindo, Ecuador (Rivet!); Germain, 1910, Miss. Arc de Méridien équatorial, **9** (3), pp. C14–C15, pl. 2, figs. 8–10.

Range.—Pacific lowlands from Tumaco Island, Nariño, Colombia south to Río Jubones basin, up to at least 3,500 feet elevation at Paramba and Huigra, probably 7,500 feet at San Jose de Minas and Ibarra. Also reported from Mera, Topo and Napo on the Atlantic slopes.

Material.—Ecuador (CNHM 132557, Zurich, Edinburgh): Mera (CNHM 86700, Jackson 7853); Napo (CNHM 117857); San Jose de Minas, Upper Guayllabamba at 2,000–2,500 meters (ANSP); Paramba (CNHM 40645, SMF 82574, Edinburgh); Ibarra (CNHM 70909, Jackson 9737); 6 miles below Huigra (ANSP 157073, CNHM 78830); between Manglaralto and Naute (USNM 517607); between Quevedo and Calceta, Manabi (USNM 534078); Val de Pilatón (USNM 307397, ANSP 82702, CM 62.4041); Bucay, Pr. Guayas, 1,000 feet elevation (ANSP 148445); Río Macima, Río Marone (SMF 15631); Chimbo (Edinburgh); Cerro Masvale, Prov. Guayas (USNM 534045); Milpe (Jackson 5103, ANSP); Sigchos (Jackson 9729); Mindo (Jackson 5116); Santo Domingo de los Colorados (Jackson 9743); Topo (Jackson 7434); lowlands of Guayas and Manabi (MCZ 139888). *Colombia* (ANSP 30645). NARINO—Río Rosario, east of Tumaco (CNHM 133262).

Diagnosis.—Basal lip with a single broad ridge, rarely with two indistinct denticles; lower palatal lip with a large, crescentic lamella extending back into aperture and marked by a deep sulcus behind lip; rarely a small accessory palatal tooth located on periphery (fig. 56b);

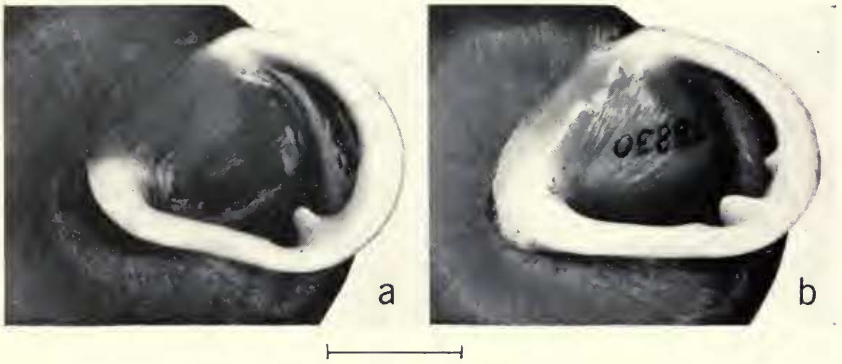


FIG. 56. Apertures of: *a*, *Isomeria globosa*, Mera, Ecuador, CNHM 86700; *b*, *Isomeria globosa* form *kobeltiana*, Huigra, Ecuador, CNHM 78830. Scale line equals 10 mm.

umbilicus closed to partly open; periphery obtusely angulated with lighter color band, spire quite elevated; parietal callus varying from thin to with a broadly raised, thick edge; surface with granulations and fine to moderately prominent striae, rarely with malleations; lip white, rest of shell dark liver brown. Diameter 32–51.8 mm. (mean 42.3 mm.), H/D ratio 0.472–0.591 (mean 0.527).

Remarks.—Germain's excellent figures (*loc. cit.*) are unquestionably of *globosa* and not of *equestrata*. The specimen he illustrated seems to be intermediate between typical *globosa* and variety *kobeltiana*. In typical *globosa* the umbilicus is narrowly to partly open, the parietal callus is very thin and without raised edges and the surface sculpture is much finer and without malleations. In form *kobeltiana* the umbilicus is closed, the parietal callus has a thick, broad raised edge and the surface sculpture is much stronger.

The only specimens that matched the type description of *kobeltiana* were from below Huigra, Ecuador (ANSP 157073, CNHM 78830). Most of the other examples were intermediate between *globosa* and *kobeltiana*. While the latter may eventually be given subspecific status, present data suggests it is only an extreme variant.

Earlier authors, utilizing *Helix* in an extremely broad sense, had considered that *Carocolla globosa* Broderip, 1832 was a homonym of

Helix globosa Sowerby, 1818. Under Article 59, Section (c) of the International Code of Zoological Nomenclature, they are not homonyms and we must return to Broderip's earlier name, rather than the familiar *subcastanea*.

Isomeria globosa has a quite wide range at low to intermediate elevations on the Pacific slopes of Ecuador and has been reported from three locations in the upper Amazonian drainage. The southern limit is very uncertain, since practically no collections of mollusks are known from northern Peru and Ecuador below the Río Jubones basin. Despite the wide geographic range, there is very little shell variation, much less than was seen in other species. Variation in one large set is summarized in Table XV. The distribution of the diameter was quite clumped with the largest a shell from "Guayaquil" and the two smallest coming from what is obviously a dwarfed population in the isolated Cerro Masvale, Guayas Province. Variation in the H/D ratio was larger, but not unusual.

Diameter in mm.	33	35	37	39	41	43	45	47	49	51
No. of specimens	2	0	0	7	22	33	9	2	0	1

H/D ratio	0.477	0.492	0.507	0.522	0.537
No. of specimens	3	3	16	17	20

H/D ratio	0.552	0.567	0.582	0.597
No. of specimens	8	5	0	2

The lower palatal lamella with its posterior indention is much larger than the tooth in any other species of *Isomeria*. When combined with the lighter zoned periphery, it at once identifies this species. Since *globosa* is the only lowland *Isomeria*, the greater development of the lower palatal tooth may reflect the need for protection from lowland predators.

NOMINA DUBIA

Isomeria calomorpha (Jonas, 1839)

Helix calomorpha Jonas, 1839, Arch. f. Naturgesch., **1839**, p. 341, pl. 10, figs. 3–4—Locality unknown; Pfeiffer, 1848, Monog. helic. viv., **1**, pp. 315–316; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 361.

Helix (*Isomeria*) *calomorpha* Jonas, Pilsbry, 1889, Man. Conch. (2), **5**, p. 142, pl. 47, figs. 31–32.

Pleurodonte (*Isomeria*) *calomorpha* (Jonas) Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Remarks.—The type of this unlocalized species is unknown and the original figures are obviously distorted. It is an unidentifiable name and can be considered a *nomen dubium*. Of the species of *Isomeria*, the most probable identification is with *I. aequatoriana* (see p. 184), but nothing would be gained by synonymizing the two. Unless the missing type of *calomorpha* is discovered, the name should be ignored.

Isomeria fauna (Philippi, 1851). Figures 53f, 54d.

Helix fauna Philippi, 1851, Zeits. f. Malak., **8** (2), pp. 29–30—Mts. near Santa Fe de Bogotá, Colombia; Pfeiffer, 1853, Monog. helic. viv., **3**, pp. 257–258; Pfeiffer, 1854, Syst. Conch. Cab., I (12), **3**, p. 416, pl. 148, figs. 1–3 (plate issued in 1853).

Helix (*Isomeria*) *faunus* Philippi, Pilsbry, 1889, Man. Conch. (2), **5**, pp. 137–138, pl. 46, figs. 21–23.

Pleurodonte (*Isomeria*) *faunus* (Philippi), Pilsbry, 1894, Man. Conch. (2), **9**, p. 94.

Range.—Known only from the type locality.

Material.—Colombia: "Santa Fe de Bogotá" (ZMA, Zurich, ex Hoffman, 1851).

Diagnosis.—Basal lip with a low swelling; lower palatal lip with small conical tooth; umbilicus moderately open; periphery acutely angulated, protruded; surface with fine radial striae and granulations, lightly malleated near periphery; lip thin and white; color dark reddish-brown; parietal callus with strong but narrow raised edge. Diameter 47–57.9 mm.

Remarks.—The status of this species is uncertain. The original figure is of a probably juvenile shell. The two specimens examined may be paratypes. They differ from *kolbergi* only in insignificant details, primarily in having the lower palatal tooth more lamellate, the malleations weaker and in being rather large. They could, however, be mislabeled specimens of *kolbergi*, since they fall within the size range of that species. The type figure, however, shows a much more elevated shell with flatter-sided spire and thinner, straighter lips. The location of the type is unknown. Rather than prematurely synonymize this, I have chosen to leave it as an unidentifiable species.

Isomeria equestrata (Moricand, 1858)

Helix equestrata Moricand, 1858, Rev. Mag. Zool., **1858**, pp. 449–450, pl. 13, fig. 1—Moyobamba, Peru; Pfeiffer, 1868, Monog. helic. viv., **5**, p. 315; Pfeiffer, 1876, Monog. helic. viv., **7**, p. 361.

Helix (*Isomeria*) *equestrata* Moricand, Pilsbry, 1889, Man. Conch. (2), **5**, p. 151, pl. 48, figs. 45–46.

Pleurodonte (*Labyrinthus*) *equestrata* (Moricand), Pilsbry, 1894 (2), **9**, p. 94.

Diagnosis.—Basal lip without teeth; lower palatal lip with a broad conical tooth; periphery obtusely angulated (?); umbilicus slightly open; parietal callus very thin, without raised edge; surface with moderately prominent growth striae and grooves; lip white, somewhat thickened. Diameter 36 mm. (from original description).

Remarks.—The partly open umbilicus, obtusely angulated periphery and single palatal tooth identify this species. Conceivably, it could have been based on subadult individuals of *I. meobambensis* Pfeiffer. Only one specimen from Puca Tambo, Amazonas, Peru at 5,100 feet elevation (Brit. Mus. 1929.6.11.3, R. W. Hendes!, I-1926) could be this species. The lower palatal tooth is a small nodule without the upper lateral extension of *I. meobambensis*. It is 20.7 mm. high, diameter 41.6 mm., H/D ratio 0.498 with 4⅞+ whorls. Puca Tambo (77°17′W, 6°9′S) is not far from Moyobamba. The specimen could have been subadult. Without more material, I cannot decide whether *equestrata* is a valid species or a synonym of *meobambensis*.

ZOOGEOGRAPHY

DISTRIBUTION OF *LABYRINTHUS*

Currently available collections extend the known range of *Labyrinthus* from Sarapiquí, Heredía, Costa Rica (*L. triplicatus*) south to Hacienda Cadena, Dist. Marcapata, Dept. Cusco, Peru (*L. diminutus*). There are numerous records from Panama and the lowlands of Northern Colombia. Most species are known from the mountainous areas of Venezuela as far east as Caracas (*L. plicatus*), Colombia, Ecuador and much of Peru. South of Buenaventura, Valle de Cauca, Colombia, all except three records of *Labyrinthus* are from the Atlantic slopes of the mountains. In Ecuador there is one record of *L. manueli* and two records of *L. raimondii* from the Pacific drainage. No *Labyrinthus* has been found in Colombia between Victoria, Caldás and Monteredondo, Cundinamarca in Central Colombia and the Caquetá River, Putumayo in Southern Colombia. Quite possibly this is an artifact of collecting. Except for *L. manueli* (*L. isodon* group), all the *Labyrinthus* of southern Colombia, Peru and Brazil are members of the *L. raimondii* group. *L. manueli* has a rather wide range in Ecuador, while the *raimondii* series extends along the fringes of the Amazonian basin at low to medium elevations. Scattered Brazilian records from Río Juruá, Río Solimoes and Río Tapajóz in Pará only hint at the extent of Brazilian distribution.

Collections of mollusks from the main Amazonian basin are practically non-existent, hence the lack of current records has no distributional importance.

Each of the well-defined species groups shows a separate geographic pattern. The *L. isodon* complex (fig. 57) has the species with the simplest teeth in Costa Rica and the western tip of Panama (*L. triplicatus* and *L. quadridentatus*) then at lower elevations in coastal central Venezuela (*L. tamsianus*). More complex dentition is seen in *L. leucodon* from higher elevations in the coastal regions of central Venezuela and *L. isodon* from the southern end of the Sierra de Perijá. There is an early (1853) unconfirmed record of *L. leucodon* from Tovar, Mérida, Venezuela. *L. dunkeri* and *L. magdalenensis*,

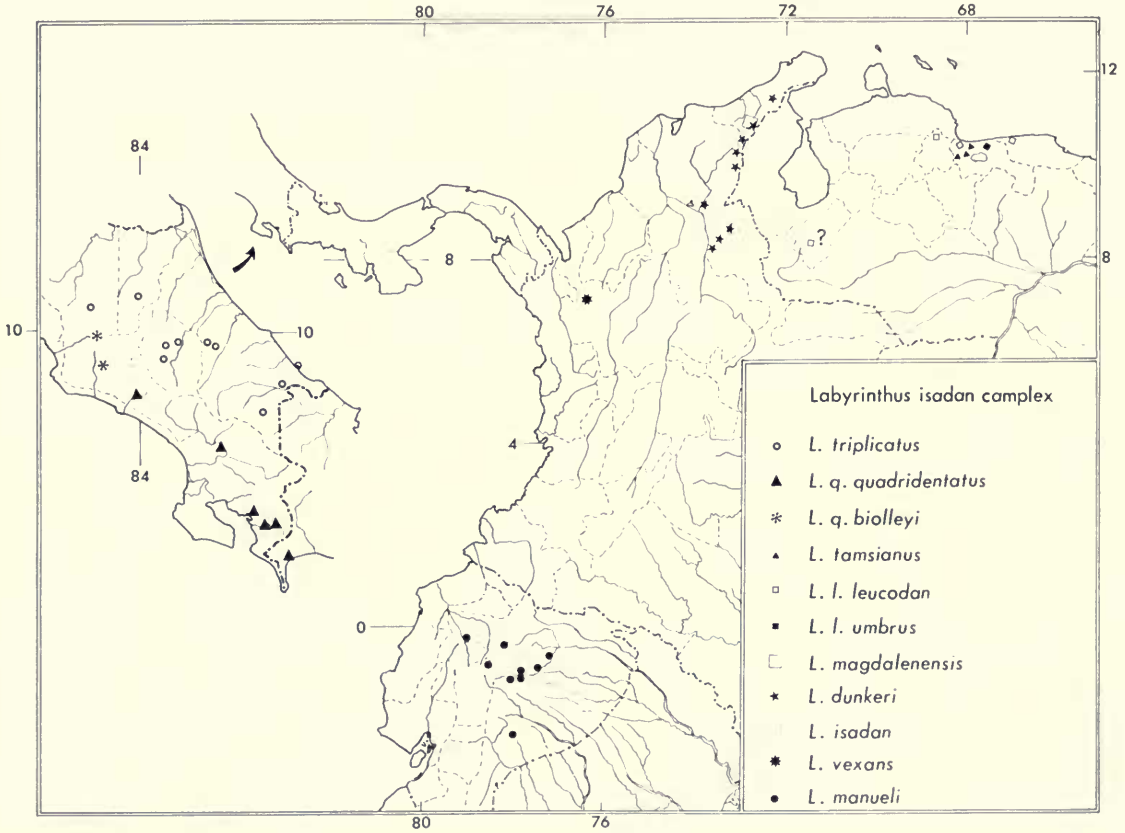


FIG. 57. Distribution of the *Labyrinthus isodon* complex.

also from the Sierra de Perijá, have quite specialized dentition. The remaining two species, *L. vexans* from Cañasgordas and Frontino, Antioquia and *L. manueli* from Ecuador could be derived from *L. isodon* with a minimum of changes and show perfect union of the parietal lamella with the lip, compared with the less perfect junction in *L. isodon*. The species near the south and central portions of the range have the most complex dentition, with those on the distributional fringes (Costa Rica and coastal Venezuela) having the least complicated dentition.

L. otostomus, apparently from the Magdalena and Cauca basins, has complex dentition easily derived from the *vexans-manueli* type, as does the very large *L. aenigmus* from Frontino, Antioquia. It is less certain that *L. clappi* from the Sierra Nevada de Santa Marta should be considered a similar development, but the general similarity to *L. aenigmus* has led to its placement in that group. Equally difficult is to determine the possible affinities of *L. sieversi*, also from the Sierra Nevada de Santa Marta. For convenience it has been grouped with the *raimondii* series, but it could be a separate derivation from the *isodon* complex. A very interesting problem is the question of why both species of *Labyrinthus* from the Sierra Nevada de Santa Marta should be imperforate, when only one of the other twenty-seven species has a closed umbilicus. With our present complete lack of ecological data, obviously no answer can be given.

Except for the already mentioned *L. sieversi*, members of the *raimondii* series are confined to the Amazonian basin (fig. 58). (*L. ellipsostomus* from "Santa Fe de Bogotá" may be an exception, although there should be slight difference between the Upper Orinoco and Upper Amazonian basin faunas). Provided the species are correctly delineated above, individual forms can show a wide geographic range, *L. raimondii* extending over a triangular area from the Upper Caquetá Drainage in Colombia south to Pucalpa, Loreto, Peru and east to the confluence of the Río Tapajóz and Amazon in Pará, Brazil. Similarly, *L. ellipsostomus* may range from the Upper Orinoco basin south to the Río Marañon, Río Juruá and east to the Río Solimões. The probable derivatives of *L. ellipsostomus* (*L. diminutus* and *L. pronus*) and the other members of the *raimondii* series are only known from Amazonian Peru at elevations of a few hundred to 7,000 feet.

L. unciger is known from low to medium elevations from Central Panama south to Chocó, Colombia just below the Panamanian border near the Golfo de Urabá. *L. creveauxianus* has been reported

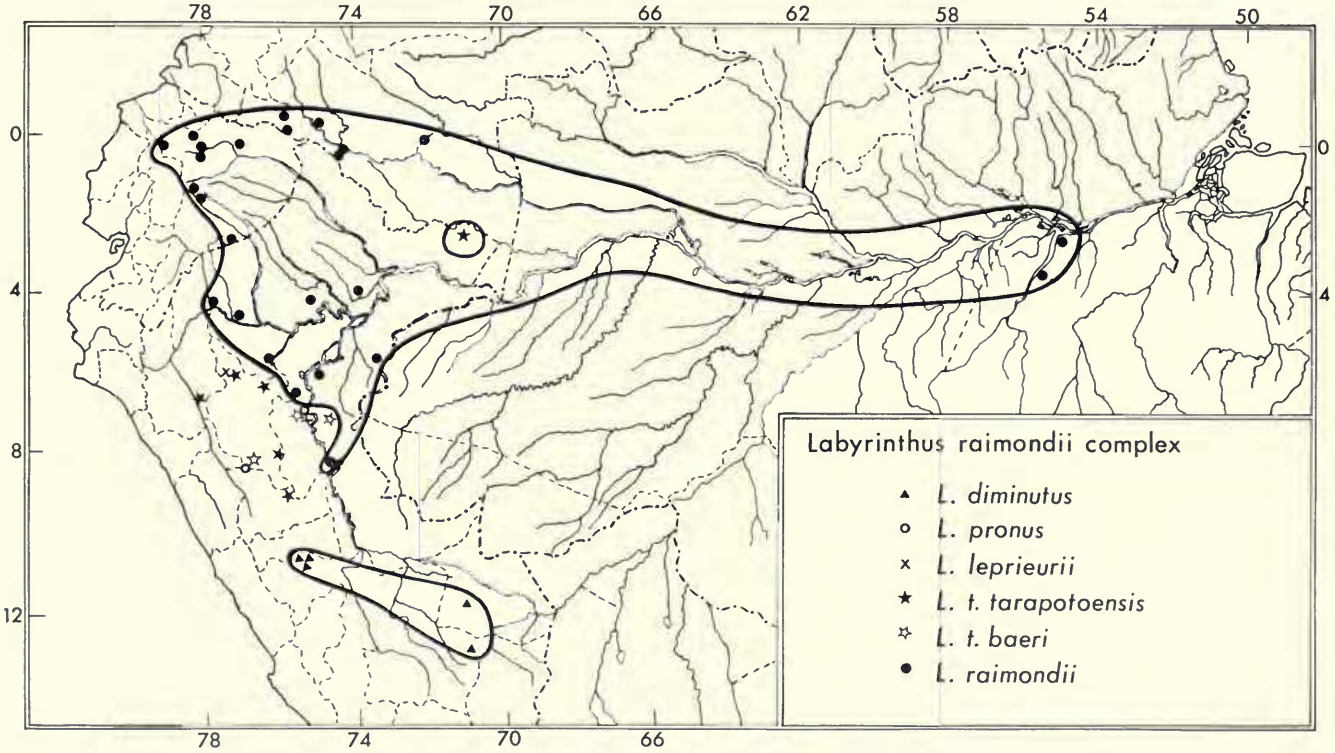


FIG. 58. Distribution of the *Labyrinthus raimondii* complex. Species without definite locality data are not included.

only from Frontino, Antioquia, Colombia, but could live at higher elevations in Darién, Panama as does a bulimulid, *Sultana* (*Clathorthalicus*) *wallisi* (Strebel, 1909) (data from Solem mss.). Several examples of *L. subplanatus* are known from the Pacific coast of Colombia as far south as Buenaventura, but no material of *L. unciger* has been taken in this region.

The remaining complex, that of *L. otis*, contains two geographically isolated species, *L. marmatensis* from the Cauca drainage and *L. plicatus* from central mountains of Northern Venezuela, and two with partly overlapping distributions (fig. 59). *L. marmatensis* and *L. plicatus* present no problems but the distribution and relationships of *L. otis* and *L. subplanatus* are still uncertain. *L. otis* is divided into two subspecies, *L. otis orthorhinus* from just south of the Panamanian border north to El Valle, Coclé Prov., and then reappearing in San José and Puntarenas, Costa Rica, and *L. otis otis* from the Pacific coast of Chocó as far south as Nuquí and then several localities around the Gulf of Urabá over to Cartagena and up the Magdalena valley as far as Barrancabermeja, Santander and Monteredondo, Cundinamarca. While no intergrades between *otis* and *orthorhinus* are known, the only fully consistent difference (presence of a deep supra-sutural groove on the body whorl of the nominate race, see fig. 31) is minor and subject to moderate variation. *L. subplanatus* is divided into three subspecies. Two of them, *L. subplanatus erectus* and *L. subplanatus sipunculatus*, range from Central Panama south to Buenaventura, Valle de Cauca and as far inland as Frontino, Antioquia. *L. s. erectus* has the more southern range with intergrades having been taken near Nuquí, Chocó. The original record of *L. s. erectus* from "Bogotá" is questionable, although not impossible. *L. s. subplanatus* is geographically isolated, having been taken in the Magdalena drainage from near Puerto Santos, Santander, upstream as far as Victoria near the Caldas-Tolima boundary. Possibly old records from Ocaña, Norte de Santander are correct. *L. otis otis* and *L. subplanatus subplanatus* have thus been collected in the same region, but not at the same locality. Similarly, *L. otis orthorhinus* and *L. subplanatus sipunculatus* have been collected from the same areas in Panama, but not at the same time by the same collector. Some specimens of *L. s. subplanatus* are very close to *L. s. erectus*, and little hesitation is felt in considering them subspecies.

The two species of uncertain status, *L. euclausus* from Zaragoza (? Antioquia) and *L. sharmani* from Alejandría, Antioquia in the

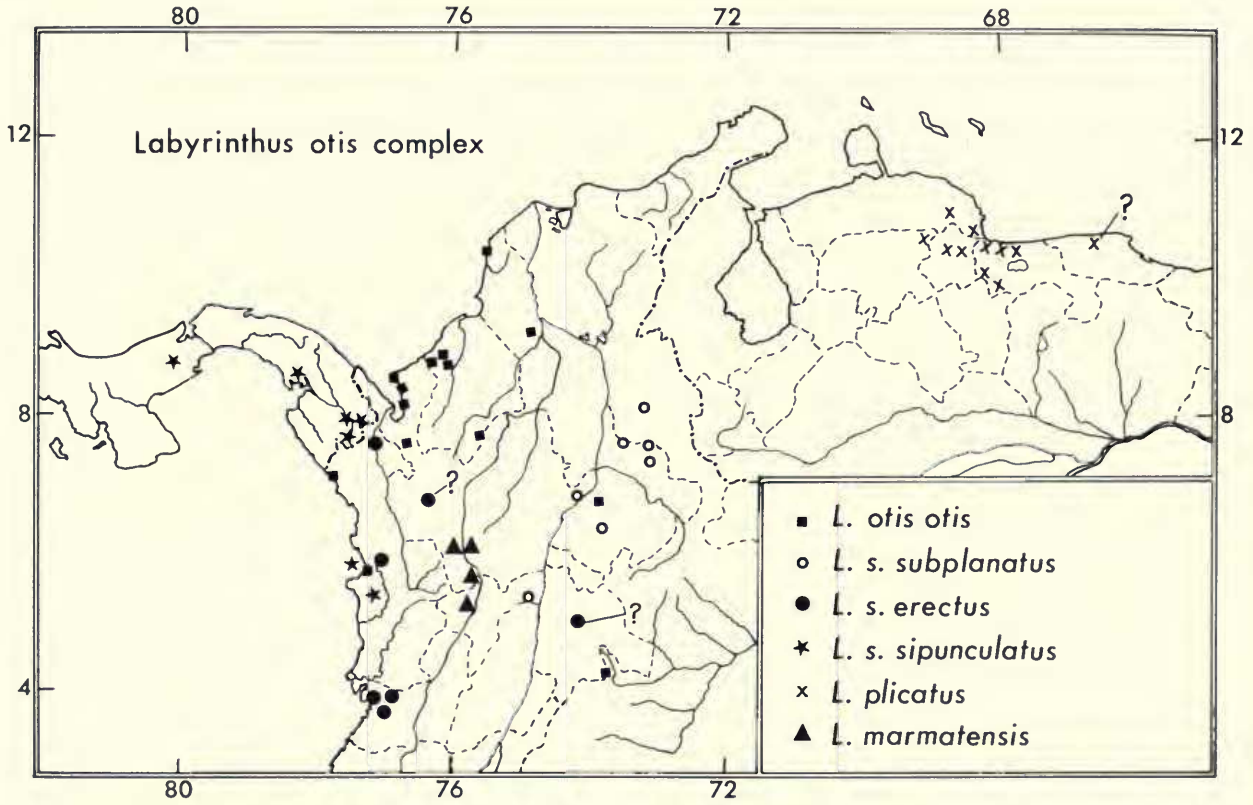


FIG. 59. Distribution of the *Labyrinthus otis* complex. The Panamanian subspecies *Labyrinthus otis orthorhinus* has been omitted in order to avoid confusion.

Cauca drainage system would not add any great extensions to the distributions outlined above.

In very few cases are there reliable records of two species having been collected at the same locality. Early records such as "Ocaña," "Chino," "Puerto Cabello," "Meobamba," "Bogotá," etc. represent only the point of purchase by early collectors and can cover a great territory of collecting activity. Even modern collections from Cerro Campana, Panama, Acandi, Colombia, or Nuquí, Colombia made by different people over a period of years can easily have come from ecologically diverse situations. The geographic name is no guarantee that the two species can be found living under the same ecological conditions in a particular patch of forest. H. B. Baker (1926, pp. 16–21) collected *L. tamsianus* and *L. plicatus* at different localities in Venezuela. Thompson (1957, pp. 5–7) reported *L. plicatus* and *L. leucodon umbrus* from Rancho Grande, Aragua, Venezuela, but the specimens were collected by herpetologists in a series of visits and easily could have come from different ecological zones. There are two situations where museum collections contain material of two or more species taken at the same locality by one collector during the same trip. *L. magdalenensis* and *L. dunkeri* were found by M. A. Carriker at Tierra Nueva, Sierra Negra, Magdalena, Colombia between 3,700 and 5,000 feet elevation. No ecological data accompanied the shells, which were collected alive or just after death. *L. leprieurii*, *L. pronus* and *L. tarapotoensis baeri* were collected by G. Rozanski at Doma Santa Clara, 6°55′S, Ucayali Valley, Loreto, Peru. The shells were all dead, worn examples and could have come from river drift.

In February 1959 I collected aestivating *L. unciger* and *L. otis orthorhinus* from under the same log in the restricted patch of forest behind the Club Campestre, El Valle, Coclé Province, Panama. The species were moderately common in the forested area, but the aestivating specimens provided no data of possible ecological differences between the two species. Unfortunately, this is the only case where two species of *Labyrinthus* can be shown to be inhabiting the same local habitat.

While there is no information about ecological relationships of members of *different* species groups inhabiting the same specific area, there are several possible cases where such a situation could be expected to exist. In the Pacific areas of Costa Rica, it is quite possible that *L. otis orthorhinus* and *L. quadridentatus* may overlap in distribution; we do know that *L. unciger* and *L. otis orthorhinus* live together in Panama; possibly *L. leucodon* and *L. plicatus* overlap in

parts of Venezuela; *L. creveauxianus*, *L. aenigmus* and *L. vexans*, representing three species groups, have been reported from Frontino; and *L. manueli* and *L. raimondii* are recorded from the same regions in Ecuador. The record cited above for museum material of two species from Tierra Nueva and three species from Domo Santa Clara are both examples of members of the *same* species group inhabiting the same area, and the variously overlapping distributions of *L. otis* and *L. subplanatus* fall into the same category. The Sierra Nevada de Santa Marta has both *L. clappi* and *L. sieversi* present, but up to now they have been taken at widely separated stations. Unquestionably, the forms delineated in the *raimondii* complex show overlapping distributions.

Thus, the quite large, easily observable *Labyrinthus* offer good opportunities for investigating the ecological relationships of closely related species, as well as species that belong to different species groups and are inhabiting the same area.

Altitudinal Zonation

Available data on the altitudinal range is summarized in Figure 60. Many of the records are based on a single collection (designated by an "X") or for an estimate from the type locality (designated by an "E"). In making the latter guesses, I have utilized data from various ornithological gazetteers giving the probable altitudinal range covered by 19th century locality records. In view of the scanty data and the diverse ecological conditions prevailing over the range of *Labyrinthus*, the importance of altitudinal range is not great, and the meaning of the differences impossible to assess. The following few comments are intended only as a guide for possible investigations.

From over 4,000 feet	From under 600 feet
L. TRIPLICATUS	*L. TRIPLICATUS*
L. SIEVERSI	*L. quadridentatus*
L. magdalenensis	*L. tamsianus*
L. dunkeri	*L. SIEVERSI*
L. tarapotoensis	*L. leprieurii*
L. PRONUS	*L. ellipsostomus*
L. vexans	*L. manueli*
L. aenigmus	*L. PRONUS*
L. clappi	*L. diminutus*
L. otostomus	*L. raimondii*
L. sharmani	*L. unciger*
L. creveauxianus	*L. OTIS*
L. OTIS	*L. subplanatus*
L. marmatensis	*L. plicatus*

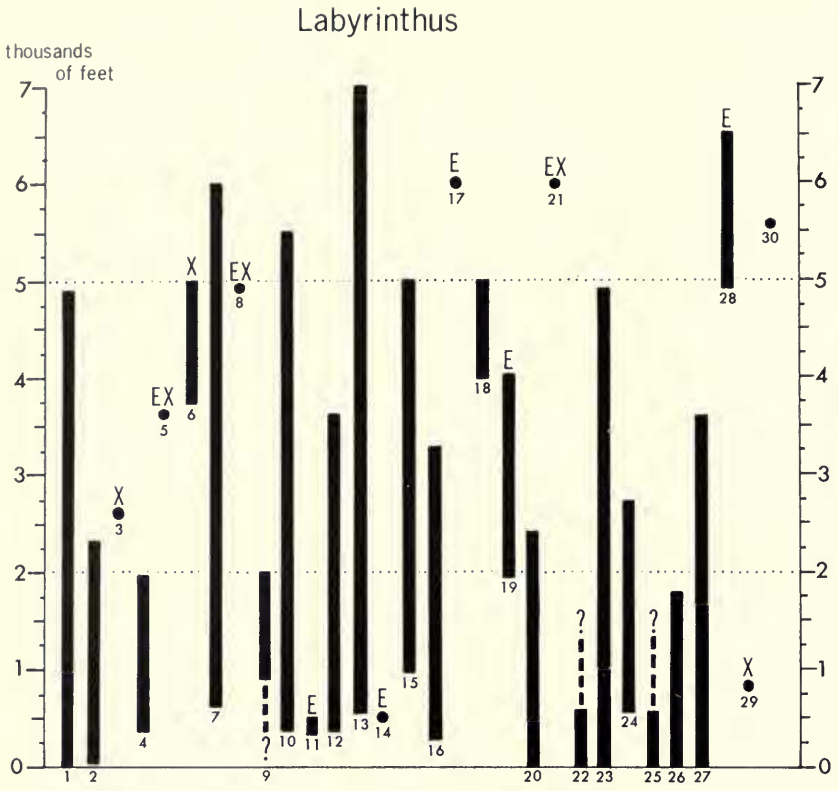


FIG. 60. Altitudinal range of *Labyrinthus*. The species are:

1. *L. triplicatus*
2. *L. q. quadridentatus*
3. *L. q. biolleyi*
4. *L. tamsianus*
5. *L. leucodon umbrus*
6. *L. magdalenensis*
7. *L. dunkeri*
8. *L. vexans*
9. *L. manueli*
10. *L. sieversi*
11. *L. ellipsostomus*
12. *L. diminutus*
13. *L. pronus*
14. *L. leprieurii*
15. *L. t. tarapotoensis*
16. *L. raimondii*
17. *L. aenigmus*
18. *L. clappi*
19. *L. otostomus bogotensis*
20. *L. unciger*
21. *L. creveauxianus*
22. *L. o. otis*
23. *L. o. orthorhinus*
24. *L. s. subplanatus*
25. *L. s. erectus*
26. *L. s. sipunculatus*
27. *L. plicatus*
28. *L. marmatensis*
29. *L. euclausus*
30. *L. sharmani*

"X" indicates only a single record; "E" an estimate based on evaluation of early ornithological collections.

Of the thirty recognized species, four (*L. isodon*, *L. bifurcatus*, *L. furcillatus* and *L.* sp.) are not sufficiently localized to give any guess as to altitudinal range. Of the remaining twenty-six species, fourteen have been recorded from over 4,000 feet elevation and fourteen from less than 600 feet elevation. Four species (in capitals) occur on both lists.

There are shorter lists of species known only from over 3,500 feet or from under 3,000 feet.

From over 3,500 feet	From under 3,000 feet
*L. leucodon umbrus**	*L. quadridentatus*
*L. magdalenensis**	*L. tamsianus*
*L. vexans**	*L. leprieurii**
*L. aenigmus**	*L. ellipsostomus**
L. clappi	*L. manueli*
*L. sharmani**	*L. unciger*
*L. creveauxianus**	*L. subplanatus*
L. marmatensis	*L. euclausus**

All those followed by an asterisk (*) are reported from only one elevation or exact locality. This applies to almost all of those recorded only from over 3,500 feet and to three of the eight recorded only from under 3,000 feet elevation. Even in the case of *L. clappi*, all recorded material was taken by Herbert H. Smith in 1900–1902 and there have been no subsequent collections. Hence the altitudinal range can hardly be considered well-defined.

A number of species are known to have a considerable vertical range. Ranked in order from largest down, giving the recorded range in feet, they are:

Recorded vertical range of *Labyrinthus*

L. pronus—6,445′	*L. plicatus*—3,600′
L. dunkeri—5,350′	*L. diminutus*—3,300′
L. sieversi—5,170′	*L. raimondii*—3,000′
L. otis—4,900′	*L. quadridentatus*—2,600′
L. triplicatus—4,850′	*L. unciger*—2,400′
L. tarapotoensis—4,025′	*L. subplanatus*—2,100′

These figures clearly show that, in general, *Labyrinthus* is an inhabitant of lowlands or only moderately elevated areas. Nearly all of the species for which a number of modern collections are available have an altitudinal range of over 3,000 feet. While several species have only been collected at altitudes of over 3,500 feet, they are all based essentially on one collection. We thus have no idea whether they reach much higher or lower altitudes. Only seven of the thirty species have been reported from over 5,500 feet. This is in marked con-

trast with *Isomeria*, which is generally found at much higher elevations in the Andes, only reaching lowland situations on the Pacific slopes, where *Labyrinthus* is absent.

Distribution of Isomeria

The center of distribution for *Isomeria* is the area from the upper Río Esmereldas basin of Ecuador across the Andes to the Napo and Pastaza drainages on the Amazonian slopes. A few species extend south to the Catamayo Valley and three species are known from Peru —*I. meobambensis* from "Moyobamba"; and *I. anodonta* from Prov. Jaén and *I. stoltzmanni* from Dist. Chota, both in Dept. Cajamarca. Only one species reaches the Pacific lowlands, *I. globosa*, which ranges from Tumaco Island, Nariño, Colombia south to the Río Jubones basin in southern Ecuador. In Colombia, most species are known from the Río Cauca basin and Cordillera Central as far north as Angelópolis, Antioquia. Surprisingly, the only records for the Magdalena basin are from the headwaters of the Río La Plata in Huila (*I. scalena*); Caldas, Tolima and Cundinamarca in the central region (*I. continua* and *I. minuta*); and the meaningless "Bogotá" (*I. basidens basidens, I. continua*). Two species, *I. oreas* and *I. continua*, have been collected in the vicinity of Villavicencio, Dept. Meta, Colombia in the Upper Orinoco Basin. Records based on material in old collections for Frontino, Antioquia (*I. oreas*) and Ocaña, Dept. Norte de Santander in the Sierra de Perijá (*I. continua, I. fordiana*) require confirmation. Finally, there are the isolated records in the Sierra Nevada de Santa Marta (*I. inexpectata, I. medemi*).

The amount of distributional data is surprisingly meager. The following species lack any authenticated locality—*I. basidens basidens, I. neogranadensis, I. morula, I. meobambensis, I. meyeri* and *I. triodonta*. Several other species are known only from the type collections, have not been found subsequently, and the exact locality where the type was collected is uncertain—*I. aloagana, I. gealei, I. stoltzmanni* and *I. fordiana*. The recently described *I. anodonta, I. medemi, I. minuta* and *I. inexpectata* are known only from the types and *I. basidens gudeana, I. aequatoria* and *I. scalena* have been reported only from localities that are within a few miles of each other. Thus, seventeen of the twenty-nine species and subspecies are based on material from essentially one locality; eleven of these do not have a restricted type locality; and thirteen are based on a single collection. Three of the remaining twelve species are Colombian: *I. subelliptica* from Buga and Cali, Valle de Cauca; *I. continua* from Manzanares,

Caldas east to Villavicencio, Meta; and *I. oreas* from the Cauca basin and vicinity of Villavicencio. Two of the nine Ecuadorean species have restricted distributions; *I. hartwegi* in southern Ecuador between Guayaquil, Cuenca and the Catamayo Valley and *I. aequatoriana* on the Amazonian slopes of the Andes from the Río Coca in the North to Méndez on the Upper Río Paute in the south. The remaining seven species have basically overlapping ranges, living in the basin of the Upper Río Esmereldas tributaries and over to the Upper Río Napo and Río Pastaza drainages on the Amazonian side.

Of these, *I. juno* and *I. cymatodes* have the most restricted range, having been reported from the area between Nachiyacu, Mera and Nanegal. *I. bourcieri* has been found in the same area and as far north as Otovalo; *I. jacksoni* from Ibarra south to Sigchos and near both Nanegal and Mera; *I. kolbergi* from Ibarra to Cayandeled, Nanegal to Sigchos, and Napo to Mera. *I. bituberculata* has been reported from Ibarra to Chimborazo, which is almost as far south as Cayandeled, and also in the Esmereldas and Amazonian drainages. *I. globosa* is known from Milpe, Topo, Mera and Napo in the Amazonian area, Paramba and Huigra in the middle elevations on the western slopes of the Andes and the Pacific lowlands from Tumaco Island, Colombia south to Albañín, Río Jubones, southern Ecuador. In addition to these rather well-known species, *I. aloagana*, *I. morula*, *I. meyeri*, *I. aequatoria* and probably *I. triodonta* presumably live in the same general area.

It must be remembered that recorded localities are valid only for the general vicinity of the cited place and probably cover a number

TABLE XVI

Trans-Andean Distributions in Central Ecuador

	Ibarra	Nanegal	Mindo	Sigchos	Nachiyacu	Napo	Topo	Mera	Puyo
I. bituberculata	X	X	X			X	X	X	X
I. juno		X			X			X	X
I. bourcieri		X	X	X		X	X	X	X
I. kolbergi	X	X	X		X	X	X	X	X
I. jacksoni	X	X		X			X	X	X
I. cymatodes		X		X		X	X	X	X
I. globosa	X		X	X		X	X	X	
I. aequatoriana					X	X	X	X	X
L. raimondii			X		X	X		X	X
L. manueli						X		X	X

of diverse ecological situations. It is very probable that distinct ecological differences separate the seven species with a trans-Andean distribution. They do have overlapping ranges with many species having been reported from the same areas on both Atlantic and Pacific sides. In Table XVI the joint occurrences of the trans-Andean species plus *I. aequatoriana* (restricted to the Atlantic slopes) and the two *Labyrinthus* known from the area are listed. All ten species have been collected near Mera, nine from Puyo, eight from Napo, seven from Topo and six from Nanegal. In view of the almost total lack of reports of species of *Labyrinthus* living in the same area (see p. 196), the startling concentration of *Isomeria* in Ecuador seems even more unusual. The possibilities for ecological studies seem excellent.

In view of the general lack of distributional data, little can be said about the patterns shown by the species groups. In form, *I. inexpectata* is nearest to *I. bituberculata*, although the geographic distribution is widely separated. *I. inexpectata* in the Sierra Nevada de Santa Marta of northern Colombia is geographically nearest to the species reported from Ocaña—*I. fordiana* and *I. continua*—although not at all resembling them in form. The *I. bituberculata* group contains two groups, one from Colombia and the other from Ecuador. *I. basidens*, with two subspecies, and *I. neogranadensis*, known only from the types, are species of the Cauca-Magdalena drainages and *I. medemi* is from the Sierra Nevada de Santa Marta. *I. juno*, *I. bituberculata* and *I. bourcieri* are part of the trans-Andean fauna of central Ecuador. *I. hartwegi* has been reported from near Guayaquil, Cuenca and the Catamayo Valley of southern Ecuador and could possibly be related to the *I. meobambensis* series.

The *I. subelliptica* group shows no geographic unity. *I. subelliptica* from central Valle de Cauca; *I. continua* from Caldas to Villavicencio, Meta; *I. minuta* from the Caldas-Tolima border area; *I. morula* and *I. aloagana* from central Ecuador; and *I. anodonta* from Cajamarca, Peru might show geographic replacement, but we lack enough data.

I. meobambensis and its allies range in southern Ecuador and Peru. *I. aequatoria* has been reported only from Huigra and Cayandeled in the Río Chanchan valley; *I. gealei* from Malacatos in the Sierra de Zaruma; *I. meyeri* from an unknown locality; and *I. meobambensis* was described from "Meobamba." Each species is known from essentially only one locality.

I. oreas and its allies form the widest ranging group. *I. oreas* from the Cauca drainage and Meta; *I. fordiana* from Marmato; and *I.*

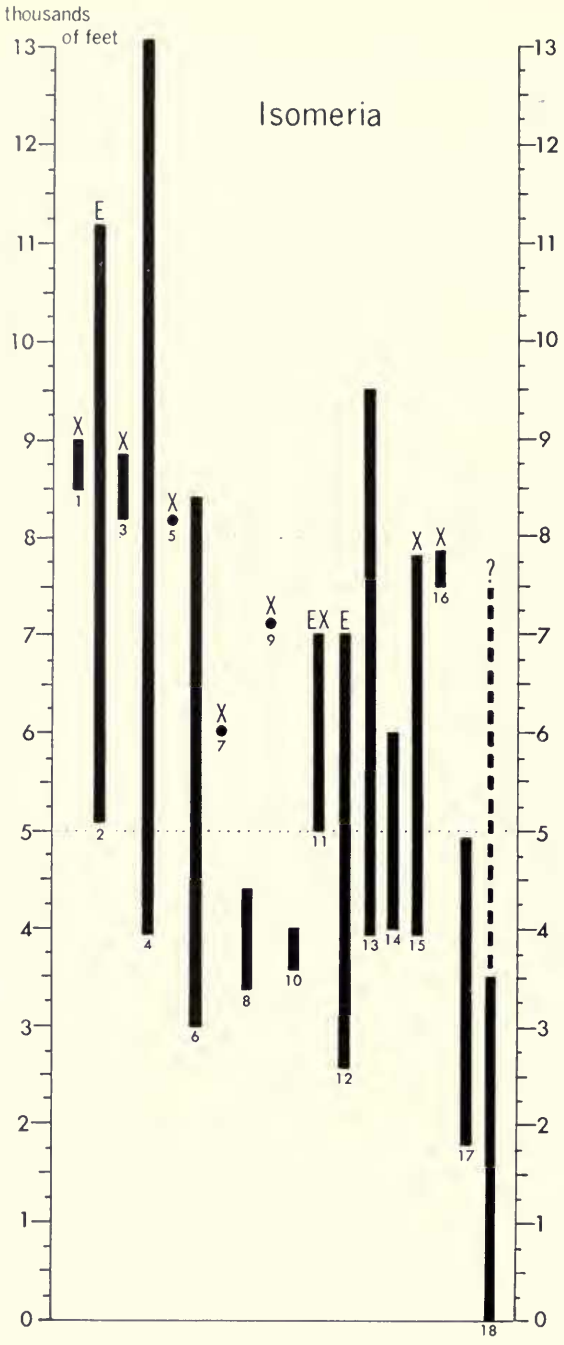
scalena from the headwaters of the Río Magdalena in Huila are Colombian. *I. stoltzmanni* from southern Cajamarca, Peru is the southernmost species of *Isomeria*. *I. kolbergi, I. jacksoni, I. cymatodes* and *I. globosa* have the trans-Andean distribution, with *I. globosa* reaching the coastal forests of Nariño, Colombia and ranging south to the Río Jubones basin in Ecuador. *I. aequatoriana* apparently is restricted to the Amazonian side of the mountains, while no localities are known for *I. triodonta*.

Altitudinal Zonation

Data on the altitudinal range of *Isomeria* is summarized in Figure 61. There are no recorded altitudes for *I. basidens basidens, I. neogranadensis, I. juno, I. morula, I. aloagana, I. meobambensis, I. meyeri, I. triodonta, I. jacksoni, I. fordiana* and *I. stoltzmanni*. Seven of the remaining species have only one recorded or inferred altitude range—*I. inexpectata, I. medemi, I. minuta, I. bourcieri, I. anodonta, I. aequatoria* and *I. cymatodes*. As in the discussion of *Labyrinthus*, in a few cases altitude records have been based on the evaluations of ornithological collections reported from the same vicinity (see p. 18).

The contrast with *Labyrinthus* is striking. Of the eighteen species with some altitudinal data, eight have not been found below 5,000 feet; seven live substantially above 5,000 feet, but have been reported at lower elevations (sea level in the case of *I. globosa*); and three species have been found only below 5,000 feet. They are distributed:

Above 5,000 feet	Above & below 5,000 feet	Below 5,000 feet
I. inexpectata 8,500–9,000′	*I. hartwegi* 3,000–8,400′	*I. continua* 3,375–4,390′
I. medemi 8,200–8,850′	*I. aequatoria* 2,600–7,000′	*I. subelliptica* 3,600–4,000′
I. basidens gudeana 5,100–11,200′	*I. globosa* 0–7,500′	*I. aequatoriana* 1,800–4,900′
I. bourcieri 8,200′	*I. oreas* 3,900–9,500′	
I. minuta 7,125′	*I. cymatodes* 3,900–7,800′	
I. anodonta 6,000′	*I. kolbergi* 4,000–6,000′	
I. gealei 5,000–7,000′	*I. bituberculata* 4,000–13,100′	
I. scalena 7,550–7,875′		


thousands
of feet
Isomeria
13
12
11
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18

Obviously, with more than half of the species without altitudinal data or only one record, the picture will change with adequate collecting. It is clear that *Isomeria* is generally found at much higher elevations than *Labyrinthus*. The only true lowland species, *I. globosa*, is in the Pacific lowlands, an area not reached by *Labyrinthus*. There is one record of *I. aequatoriana* from 1,800 feet elevation on the Atlantic slopes of the Andes. Twelve of the seventeen species of *Isomeria* with altitudinal data have been found at or above 7,000 feet elevation, which is the maximum known elevation for *Labyrinthus*. Only seven of the thirty species of *Labyrinthus* have been found at more than 5,500 feet elevation, while only three species of *Isomeria* have *not* been found at more than 5,500 feet elevation.

Comparative Remarks

Altitudinal data show a clear separation of *Isomeria* and *Labyrinthus* in most areas. In the Sierra Nevada de Santa Marta of northern Colombia, the two *Labyrinthus* have been taken at 500–5,500 feet elevation and the two *Isomeria* at 8,200–9,000 feet. In Ecuador and Peru the altitudinal ranges overlap, and at several localities in Ecuador *Labyrinthus raimondii, L. manueli* and several species of *Isomeria* have been collected in the vicinity of the same town. We have at present no information as to the ecological differences between the species and they probably will be shown to occupy distinct vegetational zones or microhabitats within the zones.

In general, both *Labyrinthus* and *Isomeria* show geographic replacement of the species, but the pattern of speciation seems to be different in the two genera and also within each genus. In *Labyrinthus*, the *isodon* series is associated with mountain masses, the species being widely separated and restricted to the foothill region and lower elevation of each separate mountain area. In Costa Rica, *L. triplicatus* of the Atlantic slopes is replaced by *L. quadridentatus* on the Pacific side. In contrast, the *otis* series shows a wider range

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Fig. 61. Altitudinal range in *Isomeria*. The species are:

1. *I. inexpectata*
2. *I. basidens gudeana*
3. *I. medemi*
4. *I. bituberculata*
5. *I. bourcieri*
6. *I. hartwegi*
7. *I. anodonta*
8. *I. continua*
9. *I. minuta*
10. *I. subelliptica*
11. *I. gealei*
12. *I. aequatoria*
13. *I. oreas*
14. *I. kolbergi*
15. *I. cymatodes*
16. *I. scalena*
17. *I. aequatoriana*
18. *I. globosa*

"X" indicates only a single record; "E" an estimate based on evaluation of early ornithological collections.

for individual species with a moderate amount of geographic overlap. Only *L. plicatus*, and to a lesser extent, *L. marmatensis* show isolation. The *unciger* series, with one lowland and one medium-elevation species, and the *aenigmus* group with its scattered species show no clear patterns of distribution. The very complex *raimondii* series may show geographic replacement in the Upper Amazonian Basin, but may equally probably be a mosaic of intergrading morphs that are partially ecologically segregated.

Being primarily a group of higher altitudes, the pattern of speciation in *Isomeria* is of geographic replacement and isolation, with the major exception of the group of species with Trans-Andean distribution in Central Ecuador (see Table XVI). Unfortunately, we do not have any data on their ecology at the present time. In the Río Paez Valley of Huila, *I. scalena* has been taken at 2,400 meters elevation and *I. oreas* at 2,900 meters. This is the only case, however, where we have any indication of altitudinal replacement in *Isomeria*.

SUMMARY

On the basis of examination of slightly less than 2,000 specimens in major museum and private collections, fifty-six species of mainland camaenids are recognized, twenty-eight of which are placed in *Labyrinthus* and twenty-eight in *Isomeria*. Four new species—*Labyrinthus magdalenensis, Isomeria medemi, Isomeria inexpectata,* and *I. minuta*—and one new subspecies—*Labyrinthus quadridentatus biolleyi*—are described and a new name (*Isomeria jacksoni*) is proposed for *Helix atrata* Pfeiffer, 1854 (not Reeve, 1852), together with many changes in synonymy. Only four species were available for dissection and only three other species had previously been studied. Anatomical variation was quite minor among the six *Labyrinthus*. The single *Isomeria* dissected differed only in having an apical appendage on the penis. All of the mainland camaenids I examined had small, hooked calcareous denticles on the interior ridges of the vagina and penis. Presumably serving a stimulatory function, no equivalent structures are known in other camaenids. The fragmentary anatomical evidence suggests a very close relationship for *Isomeria* and *Labyrinthus,* but division into two genera seems logical at this time in order to recognize the altitudinally correlated difference in apertural configurations of the shells. *Labyrinthus* is a low to moderate elevation type in which the aperture of the adult shell is strongly constricted by more or less elaborate denticles and lamellae. *Isomeria* is a group of moderate to high elevations (except for *I. globosa*) in which the apertural denticles are reduced to vestigial form or are completely absent. *I. inexpectata* and *I. minuta* are the only species tending to have characters intermediate between *Isomeria* and *Labyrinthus*. Further anatomical studies may show that the "*Isomeria*" and "*Labyrinthus*" groupings are polyphyletic and relationships cut across the present generic boundaries. Until the material needed for such studies becomes available, the present classification is a practical system recognizing a morphological and altitudinal distinction. A phyletic classification is now impossible because of the lack of anatomical material for dissection and the total absence of ecological data for the vast majority of the species.

A major conclusion to be drawn from this study is that currently available materials of Neotropical land snail taxa are totally inadequate for modern systematic studies. Most of the species and subspecies recognized here are known from a single locality or collection, 48.6% of the taxa are represented in collections by less than ten individuals and only 7.1% of the taxa by more than 100 individuals. Many of the species were collected only once during the last century and many of the type localities are sufficiently vague that they cannot be localized today within a fifty-mile radius. Despite the lack of material and data, enough evidence was obtained to suggest many intriguing taxonomic and ecological problems whose solution requires field studies. This study has been presented in its present form primarily in hope of stimulating such work. The non-marine mollusks are a difficult group to study because the level of systematic knowledge is very low, but they do offer unique biological problems and innumerable opportunities for field studies.

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